Male Movements as Honest Cues to Reproductive Quality

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Abstract

Background: Research concerning sexual selection suggests that ornaments and traits convey information that is valuable to observers when making decisions based on adaptive problems. In the animal kingdom males perform dynamic courtship displays and females assess such displays when choosing a mate. In humans however this avenue of research is in its infancy but an emerging field of study has sought to find out if dance movements, which are thought to be courtship displays, provide observers with condition dependent information.

Objectives: i) To create a methodology that records dance movements with high accuracy whilst eliminating structural cues known to influence mate choice decisions while maintaining a highly realistic human form. ii) Use this methodology to assess whether traits of interest (health, fitness, strength and age) can be detected by observers. iii) To establish if particular movements are mediating perceptions of dance quality and their condition.

Methods: A cutting edge motion capture system and professional animation software was used to record dances. Each male dancer either provided information on his health status, physical fitness, strength or age. Dance animations were shown to observers and their perceptions were correlated against the traits of interest. These were also correlated against basic biomechanical characteristics to establish possible mediators.

Results: It was revealed that whilst health measures were not related to dance ratings, strength measures were and these perceptions were mediated by movements of the upper body. A final study found that age was detectable by male participants and related to masculinity ratings of female raters but no biomechanical mediators were found.

Conclusion: Men and women are able to derive certain quality cues from observing male dance and in some instances biomechanical characteristics mediated this relationship. This provides evidence that dance may be used in the assessment of males in the context of sexual selection.

Table of Contents

List of Tables

List of Figures

Published Work

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Declaration

I declare that the work contained in this thesis has not been submitted for any other award and that it is all my own work. I also confirm that this work fully acknowledges opinions, ideas and contributions from the work of others.

Any ethical clearance for the research presented in this thesis has been approved. Approval has been sought and granted by the School of Life Sciences Ethics Committee

Name: Kristofor McCarty

Signature:

Date:

"From the invisible atom to the celestial body lost in space. Everything is movement….it is the most apparent characteristic of life: it manifests itself in all functions. It is even the essence of several of them."

Etienne-Jules Marey (1830-1904), the pioneer of motion research

CHAPTER 1: INTRODUCTION

1.1. Foundations of evolution

1.1.1 Natural Selection

Charles Darwin (1859) revolutionised the field of science with his theory of natural selection. Darwin proposed that species (and their respective traits) evolved over time via adaptation to environmental pressures as a result of natural variation. Heritable characteristics, no matter how small, that aid an organism in its survival (such as immune function, bone mass, cell structure and/or camouflage), also typically aid in the organism's ability to reproduce, and are thus passed on to the next generation. Contrastingly, characteristics that negatively impact on the survival of an organism should be phased out in subsequent generations, as individuals that possess such characters will either not be as successful in mating, or will die before they have the chance to reproduce. An organism that is successful in its fight for survival and produces more offspring, is seen as 'fit' within this framework.

However, Darwin (1859) also observed characteristics in some species that did not fit within the natural selection framework, as well as quite distinct physical and behavioural dimorphisms between the sexes despite both facing the same environmental pressures. In fact, some characteristics, especially in males, appeared to hinder the survival of the organism. Darwin's (1859) famous example of such an anomaly was that of the peacocks tail. Peacocks with large, extravagant tails were slow moving and this made them susceptible to predation. In addition to this, the physiological cost of maintaining such feathers was extremely high. According to natural selection, such extravagant features should be phased out in subsequent generations as they hindered the survival of the bird. In spite of this,

peacocks with such elaborate characters were more successful in mating than peacocks without such extravagance. These anomalies forced Darwin to formulate an additional element to the evolution framework: sexual selection.

1.1.2 Sexual Selection and differential development of mate preferences

The theory of sexual selection acts as a different selection pressure: the struggle to reproduce. The theory postulates that characteristics that are seen to hinder a given organism may in fact be providing a benefit to their ability to successfully reproduce. Darwin (1859) identified those characteristics that did not fit into the realm of natural selection, and defined them in two different ways: intra-sexual and inter-sexual selection.

Intra-sexual selection is seen as the competition between members of the same-sex (typically males) for access to mating opportunities. This often takes the form of aggression/dominance hierarchies, which lead to the development of armaments, such as antlers in stags. These physical structures are physiologically costly to produce and maintain (Kodric-Brown & Brown, 1984; Folstad & Karter, 1992; Buss, 2004; Malo et al., 2005; Mateos et al., 2008) and represent a burden if viewed by natural selection. In sexual selection however, antlers are seen as a valuable trait in male-male competitions, with successful males gaining increased mating opportunities, and subsequent genetic benefits of increased mating success.

Inter-sexual selection on the other hand is the competition to be chosen as a mate. As noted earlier, Darwin noticed that the sexes differed both physically and behaviourally from one another despite being exposed to the same environmental pressures outlined in natural selection. Trivers (1972) later hypothesised that these differences were as a result of

differences in parental investment: the sex with the higher parental investment in any offspring (i.e. the sex with the highest physiological cost) is classified as the 'choosy' sex, whereas the sex with very little investment is the 'chosen' sex. The entire theory revolves around the size and cost differences between the gametes. Female eggs are finite in number, relatively large, and incur large physiological costs to produce and nurture. Male sperm in comparison is physiologically 'cheap' to produce and theoretically unlimited. Additionally, females also incur similarly large costs in offspring development past conception in both time and the physiological costs during pregnancy, whereas a male does not need to contribute past his sperm. These large costs make females (especially mammals) much more involved in the nurturing of offspring, and as a result, females have evolved mate preferences to ensure such investment will be successful. This creates variation between male and female mate preferences. A final note however is that preferred traits such as the peacock's tail (among other ornaments such as bright plumage and long tail feathers) that were instrumental in the development of the sexual selection theory, were still not explained beyond the fact they were preferred by females. Given that the principle of evolutionary theory is the balance of costs vs. benefits, mere preference still does not provide a concrete explanation of their existence.

1.1.3 The Runaway Hypothesis

A plausible explanation for the development of ornaments did not come until 1930 with the work of Ronald Fisher. Fisher (1930) proposed the 'runaway' process, which provided an explanation as to why there seems to be a rapid development of large, exaggerated ornaments in animals such as birds and deer. The process is circular, beginning with a member of the opposite sex (typically a female) having a preference for a particular trait (for example; tail length in male birds) thus making that trait advantageous to have. Similarly, it also makes having the preference for that trait advantageous for the female. Initially, the preference for

tail length will be the functional length for flight. Males in possession of the required tail length with thus be selected for and pass this trait on to their offspring. Variation within such offspring will push the length of the tail to longer than the optimum for flight and female preference will follow suit, preferring longer tail lengths. This produces males who have decreased flight ability (due to the longer than needed tail) but with higher reproductive success, hence the term 'runaway'. This process continues until a male cannot sustain the tail length and fails to reproduce, thus causing equilibrium.

This theory postulates that these traits and ornaments are by-products of arbitrary preference by females and are not in any way indicative of male condition. There is much debate among evolutionary biologists about whether this 'runaway process' is the driving force behind these ornaments, with some researchers suggesting arbitrary preferences make for an overly unstable model (e.g. Zahavi, 1975; Hamilton & Zuk, 1982), and that more stability should be expected for such preferences to be maintained.

1.1.4 Cues and Signals

Later, a more balanced solution to the problems with the runaway process was theorised by Zahavi (1975); the reason for the development of these ornaments was in fact a form of communication (i.e. ornaments and traits served as a source of valuable information that females could detect). Many conditions of interest (such as the condition of a potential mate) are virtually impossible to measure directly, and as a result, animals (including humans) must use accessible information that is at least partially correlated with the condition being investigated. These are quite commonly referred to as signals.

These signals are monitored by receivers (for instance a female looking for condition information about a male) and in order for signals to develop successfully; they must be both detectable and actually communicate something valuable to observers. However, if a signal

does not communicate effectively or signals incorrect information (either accidental or deliberately), then it is in the interest of the receiver to ignore the signal. This forms the basis for 'honest signalling' (Zahavi, 1975; Hamilton & Zuk, 1987; Bradbury & Vehrencamp, 2011).

Some characteristics may have evolved for different purposes other than to signal information and merely correlate with the trait of interest. Observers however may still use this trait to gain insight into the hidden trait of interest in the same way as a signal but such ornamentation is known as a 'cue'. Cues are usually only partially correlated with the condition of interest (whereas signals provide more robust evidence of condition) and have typically evolved for purposes other than communication (Bradbury & Vehrencamp, 2011). For example, Bradbury and Vehrencamp (2011) note that humans cannot readily measure humidity, however one may use the related cue of sweat on another human to gauge it with reasonable accuracy. Sweat has evolved primarily to cool the body but its presence on the brow is correlated with the humidity and heat levels in the air.

1.2. Aspects of female mate choice

As the choosy sex, females have evolved several preferences for male mates that attempt to counter the offset costs females incur as a result of their higher investment, and ensure any offspring are healthy and able to reproduce.

1.2.1 Preference for health

Of primary importance to females is making sure the genes of the male she mates with are of high quality because these will be passed to her offspring (Buss, 2004). Mating with an unhealthy male has many risks for both the female and any offspring sired by him. Firstly,

unhealthy males are at higher risk of premature death, therefore ending the flow of resources (e.g. territorial defence, parenting assistance etc) he provides. Also, any offspring sired will acquire his poorer quality genes and there is a possibility that any diseases or infections the male carries will be transferred to the female, thus putting her in danger. In many avian species, a common sign that the health of a male is compromised is the presence of parasites (Hamilton & Zuk, 1987). These parasites heavily impact on the overall condition of a bird and also signify a weak immune system (Møller, 1992; Folstad & Karter, 1992). Many ecologists have observed that females have developed a preference for males without parasitic infection and look for males in good physical condition (e.g. vibrant plumage, covered in more detail in section 1.3.1). This preference holds true in many species, including humans (Hamilton & Zuk, 1987; Buss & Barnes, 1986; Møller, 1990; Gangestad & Thornhill, 1997; Shackelford & Larson, 1997; Favire et al., 2003).

1.2.2 Preference for strength and physical fitness

Closely tied to health preferences are those of physical fitness and strength. In many species, females and their offspring are at high risk of harm from predators and rely on the larger, stronger males for protection. In male gladiator frogs for example, the male is responsible for defending the nest and eggs. Before mating, a female will test the male's strength by striking him. If the male moves too much then the female leaves to find an alternative mate. In addition to external threats of survival, females often face risks of sexual domination from other males and therefore choose a stronger mate for protection (Smuts 1992). Such adaptive problems have lead to a female preference for males to be larger and have greater body strength. In addition to these traits, males that hunt have a higher cardiovascular capacity (Manning & Taylor, 2001; Manning, et al., 2007).

In humans, women consistently indicate a preference for men who are both taller and have greater physical prowess (Cameron, et al., 1978; Ellis, 1992; Buss & Schmitt, 1993) in order to protect them from other men (Smuts, 1985) and to acquire and defend important resources such as food/water and shelter.

1.2.3 Preference for resources, financial prospects and high social status.

Females also look for mates who have the potential to provide important resources such as food and shelter. Females therefore look for indicators of this potential such as social status, dominance behaviours, and in humans, earning potential. Classic examples of these behaviours are seen in mammals, where territory is often contested, and highly social animals such as primates and humans. In red deer for example, females mate with males who successfully defend their territory from other males (Carranza, 1995; Charlton, 2008).

The desirability of social rank and status is readily observed in human societies. In human history, males with the highest social status were the ones with the highest caches of food thus making them desirable as mates (Buss, 2004) which in turn created highly 'despotic' societies (Betzig, 1986). Those males with high despotic power use it to further their and their relatives' reproduction, a tendency that is still prevalent today (Summers, 2005). In the modern western world for example, American women rate success in a profession, possession of a promising career, education and professional degrees as highly desirable (Buss 2004; Buss & Schmitt, 1993) because of their high correlation with earning potential. Women in many other modern cultures also rate social status as very important in prospective mates (Buss, 1989).

1.2.4 Preference for older males

Females have also developed preferences for relatively older mates. A popular view on age is that older males have proven survival skills, as the fact a male has merely survived is proof of his genes being robust. In many species, psychological/physiological traits that are seen to be desirable and related to condition are also positively correlated with age. For example; birdsong repertoire size, vocal spectrum size and consistency of repeated notes are typically positively correlated with the age of male birds because they require good condition and learning capacity.

Another trait that is typically found in older males is their ability to acquire resources. In highly social creatures such as primates and humans, age is associated with higher social rank (Buss, 2004). In humans especially, monetary income (the modern resource) generally increases with age (Jencks, 1979). This age-resource relationship is thought to stem from our hunter-gatherer past as older males tend to be physically stronger (estimated to peak late twenties-early thirties) and more skilled hunters. Age (and its related benefits like resource potential) is reflected in women's mate preferences across a range of cultures (Buss & Schmitt, 1993).

1.3. Female mate choice in action

A common feature of many of these female mate preferences is that they are not directly observable and must be inferred from physical or behavioural characteristics of the male (i.e. they need to be signalled or cued in some way). This has led a multitude of researchers to investigate whether the ornaments that puzzled Darwin are in fact signals of mate quality.

1.3.1 Honest signals in mate choice

Researchers such as Zahavi (1975) extended Fisher's model by suggesting that in order to attain a degree of stability between a trait and its desirability, the trait must have some kind of deeper meaning aside from being aesthetic, because the pressure natural selection would exert on such a handicap would prevent survival. Zahavi (1975) proposed that the ornaments Darwin was unable to explain might for example convey information about a male's physical condition in an honest way (i.e. such ornaments signal reliable information about a male's condition and cannot be faked). This 'honesty' would help balance the trade-off between ornament and handicap as it informs the female that she is getting a higher quality mate. Furthermore, this honest signalling helps the male as he is better able to advertise his superior quality, and is therefore able to attract and mate with more (or better quality) females.

There is a wealth of empirical research that has investigated the validity of the honest signalling hypothesis and many of the findings fit well within Zahavi's (1975) model. The most prominent species of study appear to be birds, especially those with brightly coloured plumage, with researchers proposing that plumage is an honest signal of male immunocompetence, or how robust his genes are to environmental pressures. One of the first observations researchers have made to support the signalling hypothesis is that typically females (as the choosers) do not have ornaments whereas males do. This goes back to the work of Trivers (1972) on parental investment, in that males are the advertisers (hence the ornaments) and females the choosers. E.g. many female birds are monochromatic in plumage whilst the males are bright in comparison.

Hamilton and Zuk (1982) proposed that plumage in birds is related to current parasite load, and that lower parasite loads lead to more expression in sexual ornaments as the burden on the male is lower. In short, health was conveyed honestly by these secondary sexual

characteristics, and females use these as an indicator of mate quality. In order to test such a theory, Møller (1988) investigated swallows. He identified that the length of a male swallow's tail was a sexual ornament and hypothesised that the longer the tail (i.e. the more extravagant the ornament), the higher the mating success. Experiments showed that males with elongated tail feathers sired more than twice as many offspring in a single season. Møller thus concluded that such ornaments have been maintained by sexual selection and fit into the genetic quality model.

Borgia and Collis (1989) looked at satin bowerbirds (*Ptilonorhynchus violaceus)* in order to test the Hamilton and Zuk hypothesis (1982). This species of bird is a perfect test of the handicap/good genes hypothesis because the males provide no more than their genes in mating, and have varying brightly coloured plumage. Adult males have a blue plumage whereas females and younger males have green feathers. During courtship displays, sunlight refracts off the male plumage creating large flashes of light thus attracting females. The authors predicted that females would prefer darker plumage as it allows them to see the contrastingly light coloured ecotoparasites (lice) present on the birds. Moreover, the dark plumage seems to begin to develop around the eyes, where many of the parasites reside. Males with higher amounts of such parasites indicate lower resistance to disease. The data collected supported the prediction that females preferred to mate with males with lower parasite load and showed a preference for the darker plumage. This finding seems to hold across bird species; more recent research into plumage using a different species (e.g. house finches [*Carpodacus mexicanus]*), found negative correlations between parasite load in males with plumage condition (Thompson, et al., 1997).

Another, more direct method in which ecologists have investigated the honest signalling hypothesis is by directly measuring immune response to a chosen antigen (otherwise known as a 'challenge technique'). They then compare the quantified response to

ornament size and/or mating success. There are two main forms of immunity (otherwise known as strands of the immune system): cell-mediated and humoral. While humoral immunity uses antibodies that identify and combat foreign bodies, cell-mediated immunity relies upon macrophages, natural killer cells and T-lymphocytes in response to antigens.

Researchers such as Faivre et al., (2003) used a comprehensive challenge technique looking at both strands of the immune system in order to investigate a possible relationship between immunocompetence and the bill colour of the European blackbird (*Turdus merula*). The bill colour and eye-ring of male blackbirds is a yellow-orange colour whereas in females, it is brown. This is seen as a sexual ornament and it has previously been found that females prefer to mate with males with more orange-coloured bills. Furthermore, some research suggests that higher-parasite loaded males (an indicator of low imunocompetence) had paler bill colours, which they concluded meant that bill colour was a reliable index of immunocompetence. Faivre et al. found that cell-mediated (T cell) immune response was positively correlated with bill colour (i.e. the more orange the bill, the higher the response). The authors suggested that bill colour was therefore an honest signal of cell-mediated immune function, as only males of higher quality could withstand the cost on the immune system. The authors also discovered that a secondary humoral immune response (14 days after the initial response) was negatively correlated with bill colour during the breeding season. Although this initially seemed to go against the hypothesis that ornaments indicate higher immune function, it does however fit well with the handicap hypothesis, as it states that sexually selected ornaments are testosterone dependent, which is an immune system suppressant (further considered in section 1.4). The authors concluded that bill colour was indeed an honest signal of immunocompetence, and that the negative relationship in humoral immunocompetence was due to resource reallocation during the mating season as a result of heightened testosterone exposure.

1.3.4 The use of multiple signals and the introduction to cues

Although evidence from many avian species suggests that bright plumage and other ornaments are selected for, possibly based on underlying condition benefits in males, Møller (1990) criticised the hypothesis that bright plumage reliably informs females of parasite load. Some studies have found that plumage only marginally increases the likelihood of a female mating with a non-infected male, suggesting that other displays are also considered in the drive to select for good genes.

One might presume given the diversity of traits thought to be important in sexual selection that there are different signals for each trait of interest. Many researchers present evidence for the use of multiple cues however there are different theories as to whether observers use different signals for different traits (multiple messages hypothesis) or use multiple signals to assess common traits of interest in order to reduce uncertainty (redundant signals hypotheses). There is empirical evidence for both hypotheses, for example Jawor and Breitwisch (2004) found that in male Northern Cardinals (*Cardinalis cardinalis*) (a species of bird with bright red plumage) redness of the breast plumage positively predicted body size, bill colour predicted current body condition, and birds with smaller black face masks predicted reproductive success. Other researchers have suggested evidence towards the redundant signals hypothesis suggesting that, at least to some degree, signals are not wholly accurate in advertising the trait of interest and that in some cases males may try and 'cheat' or 'fake' signals thus making the trait dishonest (Dawkins & Guildford, 1991). The use of multiple signals to inform about a single quality of interest (or perhaps overall condition) therefore is to reduce uncertainty and promote honesty (Sell et al., 2009). Sometimes qualities of interest may be signalled via multiple modalities (for example birds often use acoustic

songs in addition to vibrant plumage displays; Williams, 2001) which creates an additional benefit of needing to spend less time and energy assessing two potential mates who are similar especially if they differ on a second trait. Research on Darwin's Finches (*Geospiza fortis)* has been suggested as support for this hypothesis as a correlation between body size and plumage colouration, and the size of territory the male was under command of (Price, 1984). It is thought that these two traits are used in combination and that females use the two to gain a better picture of a male's qualities.

Much of the research outlined thus far has presented the idea that secondary sexual traits have specifically evolved for the purpose of signalling qualities of interest that cannot be directly observed. However, there is a debate as to whether these have specifically evolved for the purpose of signalling (thus fulfilling the criteria of a signal) or they have evolved for another purpose (or Fisherian runaway) and are merely a correlate of the trait of interest and is therefore defined as a cue (for full definition and examples see Candolin, 2003; Bradbury & Vehrencamp, 2011). Cues therefore fit well into the premise of the redundant or 'back up' signalling hypothesis as some error or ambiguity in the honesty of the cue is in question. Indeed in many species where conspicuous ornamentation is missing all together, the use of cues is of particular importance in order to avoid uncertainty.

1.3.5 Fluctuating Asymmetry

Many species (particularly mammals) lack conspicuous ornamentation to signal quality. This means that other characteristics should be available to females in order to convey relevant condition-dependent information. One such characteristic is that of fluctuating asymmetry (FA). Ideally, most bodily features are bilaterally symmetrical. However, there are always small deviations from perfect symmetry, and it has long been thought that such deviations are

an indicator of developmental instability. Pressures, both intrinsic (predominantly genetic) and extrinsic (predominantly environmental) are thought to disturb the expression of a given phenotype and cause 'noise' which leads to slight imperfections in development that are revealed as asymmetries (Palmer & Strobeck, 1992; Leamy & Klingenberg, 2005). Frederick and Gallup (2007) report that variance in FA is typically 60% genetic and 40% environmentally influenced. Fluctuating asymmetry has been found to have particularly strong effects on structures shaped by sexual selection because these structures are under strong directional selection (and are hence developmentally unstable) (Møller, 1990; Møller, 1993; Roldan, et al., 1997; Simmons & Hunt, 1997). Logically this leads to three key hypotheses: i) individuals that are exposed to more environmental pressures (for example temperature, chemicals, and/or lack of nutrition to name but a few) should be more asymmetrical, ii) organisms in low stress environments should have higher symmetry, iii) individuals that are more symmetrical should show greater robustness to these pressures (i.e. are in better physical condition) and should be preferred as mates in both sexes.

1.3.6 FA in Comparative Literature

As with the majority of research investigating signalling and condition dependence, considerable research has been conducted in avian species. This is primarily because birds are susceptible to a highly experimenter-controllable pressure: that of parasite loading. In order to investigate the hypothesis that external pressures do in fact play a role on tail symmetry in swallows (*Hirundo rustica)*, Møller (1992) exposed nests to varying levels of parasites (a typical physiological stressor in birds) and observed the effects in tail FA. As expected, FA increased as parasite loads were introduced. Møller also observed that the degree of FA was more pronounced in the feathers associated that are relevant for sexual preference (tail) as

opposed to other feathers, giving credence to the hypothesis that sexual ornaments convey condition-dependent information. It also provides support for the theory that FA is both sensitive to, and a reliable indicator of stressors. Similar findings are described in the work of Lens et al., (1999) who compared degree of FA in seven species of forest-restricted birds (Taita white-eye [*Zosterops silvanus]*, Taita thrush [*Turdus helleri]*, stripe-cheeked greenbul [*Andropadus milanjensis*], Cabanis's greenbul [*Phyllastrephus cabanisi]*, white-starred robin [*Pogonocichla stellata]*, yellow-throated woodland warbler [*Phylloscopus ru¢capillus]* and olive sunbird [*Nectarinia olivacea])* whose nests had been disturbed by changing environments, with that of museum specimens from 50 years before. Compared to the museum specimens, the birds currently residing in the disturbed environment showed up to sevenfold increases in FA, a finding the authors attributed to strong negative environmental stress as a result of a disturbed habitat.

Various researchers have found that symmetrical features in many bird species are preferred by females and conclude that females are using symmetry as an honest indicator of physical quality (for a review see Møller and Pomiankowski, 1993; Swaddle & Cuthill, 1994). However this conclusion may not be as clear-cut as first thought, especially with regard to avian species; Oakes and Barnard (1994) experimentally manipulated tail symmetry of male paradise whydahs (*Vidua paradisaea*), and observed the subsequent effect on mate choice. Unexpectedly, the authors found that females actually preferred males with higher FA tails. The authors suggested that this was because the manipulated tails were perceived to be longer and thus different from the norm. This however may be a result of avian species having other, more conspicuous ornamentation that command higher attention by females.

FA research is not just limited to avian species, in fact in some species where conspicuous ornamentation is missing altogether (like many mammals) some researchers believe greater attention is given to FA. Roldan et al. (1997) for example assessed reproductive

value in male gazelles (*Gazella cuvieri)* by analysing their sperm during the mating season and compared this to their FA. They found that the degree of FA was both positively related to inbreeding (Inbreeding promotes deleterious alleles that would normally be phased out), and negatively associated with sperm quality (i.e. high instances of inbreeding led to higher asymmetries and reduced the quality of sperm). This was followed up by an investigation three years later, which expanded the sample to three species of bison (*Gazella dorcas, Gazella dama* and *Gazella cuvieri),* and here the authors found that FA was a reliable indicator of male reproductive stress as it was related to individual semen quality in all three species (Gomendio, et al., 2000). FA has also been linked with antler symmetry in moose (*Alces alces gigas)* (Bowyer et al., 2001) and reindeer (Lagesen & Folstad 1998). Lagesen and Folstad positively associated symmetry level in reindeer (*Rangifer tarandus)* with the host's immune function, suggesting that FA relies upon immunocompetence, and thus is an honest signal of such condition.

FA has also been investigated in primate species. Canine teeth in particular are of interest to researchers because they have been shaped by sexual selection (specifically intrasexual selection as they are used as weapons) and so FA should have a more noticeable effect on these structures. Higher-ranking male Macaques (*Macaca fascicularis* and *Macaca fuscata)* yawn a lot exposing their teeth (Troisi et al., 1990) and in some species, males use their opponents FA to assess their phenotypic quality (Manning & Chamerlain, 1993). The development of FA in dentition is thought to be primarily genetic as their growth is largely dependent on the genome, and their development appears to be particularly resistant to environmental pressures (Frederick & Gallup, 2007). Manning and Chamberlain (1993) investigated FA in canine teeth in museum specimens of 21 species of Old World primates (including common chimpanzees (*Pan troglodytes),* gorillas (*Gorilla gorilla*) and pre-industrialised humans. It was found that in males, mean FA was significantly correlated with

measures of sexual selection such as canine size and dimorphism, causing the authors to speculate that FA in canines was used as honest signals of phenotypic quality.

1.3.7 FA in humans

More widespread research on FA has been conducted in modern humans and is thought to play an important role in perceived physical attractiveness. FA has been linked to several mating behaviours leading to assumptions that it conveys information about physical condition. As with primates, humans lack conspicuous ornamentation and are ideally bilaterally symmetrical in both the face and body. From previous animal literature, there appears to be a wealth of literature supporting the supposition that FA is correlated with the physiological condition of the organism and in some studies, is a trait that is appears to be selected for. This has provided the basis for research investigating the extent to which FA is both related to physical condition and is a trait that is preferred (usually encoded into attractiveness) in humans.

Thornhill and Gangestad (1994) tested the hypothesis that low FA should be preferred in bodies. They measured FA in seven bodily (but not facial) traits in both men and women from a college sample, and asked them how many sexual partners they had had in their lifetime. After partialling out age (as sexual partners can be expected to increase with age), significant negative correlations were found between FA and self-reported sexual partners in both men and women. Higher symmetry was thus associated with more sexual partners. It appears that more symmetrical bodies are rated as being more attractive (Brooks & Pomiankowski, 1994; Concar, 1995) so one might be tempted to conclude that bodily symmetry is used to determine physical condition by observers. However, whilst these studies provide evidence for a correlation between FA and sexual partners and attractiveness,

it would be near impossible to use body asymmetry to make mate choice decisions as clothing would conceal the cues.

The face (another ideally symmetrical body structure) however, is constantly visible and so a more likely hypothesis is that if FA is used as a cue to physical condition, it is most likely to be assessed via the face. In humans, the face is thought to be central in mate choice (Perrett et al., 1998) and in the past, standards of facial beauty were thought to be set by tightly shaped cultural conventions (Rhodes et al., 1998). However more recently, evolutionary biologists suggest that there are common visual cues that underlie attractiveness across cultures and the reason for these cues being preferred is because they might convey condition information (for example Perrett et al., 1999; Jones et al., 2001). Much of this empirical work has been investigating FA's relationship to attractiveness and results typically report positive relationships with FA and attractiveness (e.g. Rhodes et al., 1998; Perrett et al., 1999; Jones et al., 2004), especially in short term mating behaviours (Gangestad & Thornhill, 1997) because of its link to robust genes.

A key assumption of the honest signalling hypothesis is that these traits (like FA among others) boost reproductive quality. Manning, et al., (1998) looked at the relationships between FA of finger lengths and ejaculate size and sperm quality (motility) in men attending an infertility clinic. It was found that absolute FA (an aggregate measure of deviation from zero) of the fingers was negatively correlated with sperm number per ejaculate, as well as sperm speed. Furthermore, men who were being treated for extremely low (or no) sperm counts (azoospermia) were found to have a much higher degree of FA. Firman et al., (2003) also found that sperm quality was negatively related to FA of body traits (ear and foot lengths, wrist, elbow, ankle, and foot widths, as well as the lengths of digits 2-4 on the hand) in healthy men.

To a lesser extent, FA has been associated with psychological condition/health. Like physical condition, psychological health is an important consideration in women's mate choice preferences as factors such as intelligence are preferred because of its correlation with resource acquiring ability. Shackelford and Larsen (1997) assessed whether psychological and emotional wellbeing was related to FA in the face. Two samples of students (both men and women) completed various personality, depression inventory and emotional control questionnaires alongside daily diaries over a course of four weeks. It was found that men with greater facial asymmetry reported greater emotional instability and higher depression than more symmetrical men. This trend has also been replicated using FA in body traits (Martin et al., 1999) and by using IQ as a measure of psychological condition (Furlow et al., 1997)

1.3.8. FA Summary and Alternative Explanations

In summary, it appears that FA is present in many species and evidence points towards it being an honest indicator of a range of physical and psychological traits thought to be important in mate choice. However, the majority of studies report quite subtle deviations from perfect symmetry that would be particularly hard to assess in less than perfect lighting conditions or from a distance. This has led some researchers to question the plausibility that observers are actually using FA as an indicator (or signal) of condition (Møller & Pomiankowski, 1993). Swaddle (1999) for example reported a recognition threshold in European starlings *(Sturnus vulgaris*), which means they cannot discriminate FA's that are less than 1.25%. Swaddle observed that in nature, FA's are often smaller than this, and concluded that relying on symmetry alone is implausible, despite the overwhelming empirical evidence that females appear to prefer symmetrical mates. A somewhat similar pattern has been found in humans. For example Scheib et al. (1999) found that there was significant negative correlation between FA and rated attractiveness in men's faces. However when

asked to judge the symmetry of a face, they were unable to do so with accuracy. This suggests that in humans, whilst symmetrical faces are more attractive, the symmetry of the face is not directly discernable and that a similar recognition threshold (as found by Swaddle in birds) is in place.

The subtle nature of FA is in contrast to many honest cues that are extremely exaggerated and conspicuous. Both Fisher (1930) and Zahavi (1975) would argue that in time, if a cue is used as a signal of quality, it would become more exaggerated until the cost-benefit balance cannot be sustained. This suggests that FA may in fact be a by-product of the selection process or that it is taken into consideration with other, more pertinent cues of condition. To demonstrate this, Johnstone (1994) created a computational model using basic artificial neural networks that were designed to mimic the selection process of symmetrical tail feathers. This network suggested that FA is indeed a by-product of the selection process and not a signal in its own right, which provides an explanation of why it is often very subtle. He explained that in the network, the population mean FA is zero (completely symmetrical) and female preference in subsequent trials appears to prefer that of the population average, meaning that low FA is preferred even in the absence of a link with quality.

1.4. Testosterone, 2D:4D and the Male Face

Males and females are often conceptualised as being at either end of a continuum with no interplay, however this definition is not as clear-cut as initially thought. The qualities defining ‘sex’ are influenced in a number of ways aside from pure genetic and morphological differences (Neave, 2008). Unlike sex chromosomes that are digital in their makeup (with either an XX or an XY), hormones are more analogue in their excretion allowing for males for example to lie closer toward the middle of the continuum and some females to be closer

to the male end. Of interest to many evolutionary biologists/psychologists investigating mate choice, has been the role played by the gonadal sex steroids. In particular researchers have attempted to investigate the extent to which they are related to mate choice characteristics.

The principle male sex hormone is testosterone (T), secreted primarily in the testes in males. During foetal development, the foetus is bipotential during the first six weeks and can develop into either a male or female. The amount of prenatal testosterone exposure to the foetus is under control of the sex chromosomes and after the 6-week point the absence of androgens such as T will result in the development of a female. The development of males relies strongly on the secretion of T and its metabolites from week 6 onwards which further influence gene expression and the volume of exposure to prenatal testosterone. This has a marked, long-term organisational effect on the body and brain. The role of T does not stop at birth and also plays a large role in the expression and organisation of secondary sexual characteristics and male-typical behaviours that are particularly salient post-puberty. It is also linked to sperm counts (Manning et al., 1998a). In addition, T is an immunosuppressant and plays a significant role in the handicap hypothesis, as males in good condition, carrying the handicap of high T are preferred (Folstad & Karter, 1992).

The majority of research in the realm of sexual selection has placed a particular focus on the organising effects of testosterone *in utero* (prenatal testosterone or PT). Degree of exposure during foetal development appears to share relationships with traits preferred by females such as dominance, masculinisation of facial features (Neave et al., 2003), physical strength (Manning & Taylor, 2001)) and cardiovascular fitness (Hönekopp et al., 2006). Measuring prenatal testosterone directly is invasive and rarely feasible so many researchers use a proxy measure which is thought to be correlated with PT levels *in utero*: the relative ratio of the length of the second and fourth finger digits (2D:4D). 2D:4D is sexually dimorphic with men having somewhat lower ratios than women (i.e. their 4^{th} finger tends to

be long in relation to their 2nd finger). The development of both the digits and the testes in humans is under the control of the *Hox* gene family, and lower finger ratios are indicative of higher testosterone exposure *in utero* and in higher sperm levels, which is why it is speculated that 2D:4D may be related to fertility (Manning et al., 1998b).

1.4.1 Testosterone, strength and physical fitness

Selective pressures in human evolutionary heritage are thought to explain why the sexes differ in athletic performance (Hönekopp et al. 2006). This is thought to be as a result of PT's organisational effects on the cardiovascular system (Manning & Bundred, 2000) as well having steroidal effects on the muscles (Fink et al., 2006). Successful performance in many sports relies heavily upon the cardiovascular system and the muscles, and in terms of athletic performance, males typically outperform females in the region of around 10%, despite increased female participation in sport (Coast et al., 2004). These dimorphisms are most likely due to an interaction of a multitude of factors including strength, maximal oxygen uptake (VO^2Max), anaerobic threshold as well as more social factors such as training intensity and frequency (Manning & Hill, 2009). Many researchers believe however that these sex differences may have arisen as a result of T (Andersson, 1994), and its proxy measure 2D:4D has been compared to performance in number of sports and examples of athleticism in both men and women.

Manning and Taylor (2001) suggested that competitive sports might act as proxies for male-male fighting ability (i.e. intra sexual competition) because of the comparative demands they have on visual-spatial judgement, speed, endurance and strength. The authors use the example of football (soccer), as it requires all of the above attributes during a 90-minute game. A preliminary study was first conducted by correlating male 2D:4D with their

subjective ratings of ranking within their desired sport using a Likert-style scale (with 10 being of international quality). Results revealed a significant negative relationship between 2D:4D and their ranking on the scale providing preliminary evidence for a performance/PT relationship, with those ranking themselves higher on the scale having more masculinised digit ratios. A follow-up study specifically looking at both professionals and controls found that the top ranking players (who had represented their country) had significantly lower finger length ratios than controls, reserve players, and players who had yet to play for their country.

This pattern of lower digit ratio and athletic performance also holds for many other sports and activities such as endurance running (defined as continuous running over 1km), a sport where typically men are faster than women. Manning, et al., (2007) suggested that around 25% of the variance in endurance running performance can be explained by 2D:4D in both men and women. Furthermore male performance in surfing (Kilduff, et al, 2001), and fencing (Voracek et al., 2006) are also negatively related to 2D:4D which the authors attribute to both testosterone's organisational effects on the cardiovascular system, as well as the central nervous and musculoskeletal systems as these sports require precise hand-eye coordination. Other studies have attributed 2D:4D and performance in sport to the steroidal effects PT has on the muscular system (i.e. strength). Performance in handgrip strength measurements (a good correlate of overall body strength) has sometimes been found to be related to masculine finger ratios in a cross-cultural sample (e.g. Fink et al., 2006) as well as in rugby (Bennett et al., 2010), sumo wrestling (Tamiya, et al., 2012), and sprinting speed (Manning & Hill, 2009).

1.4.2 Gauging strength and fitness in human male face

Physical strength and fitness are preferred in men for the obvious survival benefits for both the man himself, as well as the ability to protect offspring and successfully hunt for food (Buss, 2004). Such abilities seem to be influenced by PT from the wealth of studies outlining relationships between prenatal testosterone, and performance in sport. Physical strength may not always be accurately discernable from body shape (e.g. obscured by clothing) and cardiovascular fitness is not directly observable from body shape, which has led to some researchers attempting to find honest cues to these traits in the face. PT has previously been found to masculinise faces in a variety of different ways, and these traits have been linked to dominance and masculine behaviours that have led some researchers to hypothesise that other traits such as strength can also be observed in the face.

Fink, et al., (2007) wanted to establish whether women could detect strength in male faces. This viewpoint pertains to strength being inter-sexually selected for the protection benefits. The authors measured male handgrip strength and displayed males' photographs to women to obtain ratings of attractiveness, dominance and masculinity. Mean handgrip strength (after controlling for height and weight) was positively correlated with all three measures, suggesting that it is possible for observers to (rather indirectly) detect strength from the face.

The evidence presented in the preceding sections makes it tempting to agree that human evolutionary heritage has developed as a result of intersexual preferences because of the lack of apparent intra-sexual conflict. However, an alternative viewpoint is that primarily strength in men should have evolved for intra-sexual purposes. From an intra-sexual point of view, the ability to gauge strength (i.e. fighting ability, formidability) before a male-male conflict seems highly logical as "decisions (to undertake conflict) have larger pay-offs when uncertainty can be reduced" (Sell et al., 2009 p.7). However, an article by Puts (2010) suggests that evidence in-fact does not point in that direction. Instead Puts argues that male

traits are better designed for intra-sexual competition and this has been the driving force for their development rather than via inter-sexual selection. Puts (2010) points out that these so-called 'desired' male traits such as increased body size, greater build and muscle mass, strength, fitness, and dominance in fact should have evolved in response to same-sex contests rather than ornaments (defined as a trait that evolved and contributes to fitness primarily through female preference). Same sex contests override other methods of sexual selection because if only winners are given access to females, then there is no opportunity for female choice (or coercion) and no need for sperm competition.

Sell et al. (2009) also stated that intra-sexual conflicts should be preceded by a visual assessment of the opponent before engaging in combat in order to gauge formidability in an effort to avoid physical conflict with much stronger males. It is thought that this cognitive architecture should be present in humans because during our ancestral heritage, evidence suggests that anatomical differences in upper body strength evolved to inflict injury on one another: Men have approximately 75-85% greater upper body muscle mass than women but only 50% greater lower body strength, for example. To test human perceptual abilities in assessing strength, the authors conducted a number of studies assessing the upper and lower body strength (measured via weight lifting machines in a gym) in both men and women and displaying either photographs of their whole body, just their faces or just their bodies to judges. Instead of the rather indirect ratings of masculinity and dominance as Fink et al., (2007) used, Sell et al. asked judges to directly rate perceived strength, and whether they thought the person would win physical fights (a measure of formidability). It was found that strength could be accurately assessed in pictures of males who regularly worked out at the gym when viewing face and body, slightly less for the body alone, and less again (but still significant) for the face only. This also held for perceptions of fighting ability, as this

measure was significantly positively correlated with the males' strength score, in particular, their upper body strength.

Two subsequent studies sought to extend this to both men and women who did not regularly work out at gyms, in addition to a cross-cultural sample of stimuli. It was found that in a culturally matched sample of stimuli and raters, similar degrees of accuracy were observed for strength perception of the whole body, body only and face only conditions in men, and whole and body only shots in women. However, accuracy diminished when rating women's faces for strength. In the cross-cultural sample, it was found that strength could be accurately gauged in the faces of both Andean and Tsimane populations. Overall Sell et al., (2009) concluded that these assessments of strength (independent of body size) were specifically related to upper body strength rather than lower body strength in fitting with the hypothesis that this perceptual ability may have evolved to assess fighting ability in men, as the upper body is most relevant to formidability.

Whilst the literature on the relationships between male strength and the face seem rather clear cut, the ability to accurately observe cardiovascular fitness seems less robust. Cardiovascular fitness, a key component in performance in many sports seems to share a relationship with PT exposure that goes towards explaining the dichotomy between men and women. Men's higher performance in cardiovascular-demanding activities is predicted to be as a result of intra-sexual conflicts and the ability to hunt (suggesting inter-sexual abilities) (Manning, 2002). Therefore, one might argue that cardiovascular fitness should be observable in a similar fashion to strength in the face to act as a cue to both men (from an intra-sexual view point) and women (intersexually). Surprisingly few studies have investigated this and the ones that have may be confounded by methodological limitations.

Hönekopp, et al., (2004) investigated whether physical fitness was visible in the facial attractiveness of women. Whilst the results initially indicated that this was indeed the case, one might argue that their measure of fitness (the Haro fitness test) measured all round fitness (encompassing cardiovascular capacity, endurance and strength) rather than just cardiovascular fitness, thus making it impossible to speculate as to its contribution to facial beauty. Similarly, Williams, et al., (2010) sought to find a relationship between performance in the National Football League (NFL) Quarterback (QB) aptitude test and facial attractiveness (as rated by women, thus tapping into intersexual mate choice) in men. Using the same theoretical underpinning that the face displays underlying condition dependent information thought to be testosterone related, they found that performance on the test (given as an overall performance score on passing) and each player's career QB rating were positively related to their facial attractiveness as rated by a sample of young women. However, NFL QBs don't just require high cardiovascular fitness, they require a great deal of strength in order to execute and overcome tackles (and thus train accordingly) meaning these ratings of attractiveness may be based on strength rather than cardiovascular fitness.

1.4.3 Summary

It appears that testosterone, particularly the organising effects of PT, are linked with male-typical characteristics such as physical strength, fighting ability cardiovascular fitness. Some of these characteristics such as dominance, cardiovascular fitness, and PT exposure are not readily observable and so must be inferred. Although it would seem that strength might be inferred from observations of build and visible muscle mass, depending on the activities one pursues this might be difficult, especially if the person is strong yet lean (for example;

dancers). The majority of research concerning the cueing of such traits has concerned the face, as it is known that many other non-observable characteristics are encoded in it.

Aspects such as strength and fighting ability seem to be observable via the face, especially when men judge male faces. This is in line with intrasexual selection theory and the markers of strength in faces also seem to be under control of prenatal testosterone. Cardiovascular fitness has been seldom researched in relation to whether or not it can be inferred from the face, with relevant studies confounding cardiovascular fitness measures with strength measures.

Aside from there being a wealth of information concerning the honest signalling capacity of static cues such as the face, very little is known about the signalling value from other types of cues. Whilst static images of faces provide very convenient laboratory stimuli that can be carefully manipulated and controlled, they fail to capture the richly dynamic nature of human life. Despite this, the use of dynamic courtship displays as a means of cueing condition dependent information in the animal kingdom is quite well documented.

1.5. The assessment of movement as an honest cue to mate quality

Some researchers have investigated the extent to which movement can signal physical condition and be used in the assessment of potential mates. From a theoretical standpoint this makes sense as i) the ability to move relies upon sensory and musculoskeletal systems, which are probably condition dependent, ii) individuals appear to be 'prepared' to respond to biological motion (considered in greater detail in section 1.6), iii) unlike very subtle cues like FA, movement is readily visible and iv) some information, particularly in the face of humans, can only accurately be conveyed via movement such as facial expressions and emotionality. However, despite this potentially rich avenue of cues, movement research has been scarcely

applied to questions regarding signalling or mate choice even though this unexplored avenue of sexual selection was identified over ten years ago (Farnell, 1999).

In real-life situations when someone is judging a potential partner's attractiveness, it is most likely (with the exception of dating websites etc) that the individual's face is dynamic, and this displays information on expressiveness, eye gaze and emotion, and is omitted when the face is static (i.e. a photograph). Rubenstein (2005) conducted experiments aimed at identifying whether ratings of attractiveness are different if the stimuli are presented differently (i.e. static or dynamic). To create the dynamic stimuli, Forty-eight females were asked to read a passage in a neutral expression in front of a video camera (variables such as hair and jewellery were covered/removed). To maintain control, the static images were taken from the dynamic trials. Both static and dynamic conditions were presented to participants in a rating component (making sure to only show each face in one format) and facial attractiveness was established. Rubenstein found that ratings of attractiveness of the static face did not necessarily correlate with ratings of the same face in the dynamic form. In conclusion, Rubenstein suggested that different evaluative standards are used when rating attractiveness depending on how the face is presented. In a second study, Rubenstein investigated the differing evaluative methods of how a face is rated to be attractive. It was predicted that features such as emotion are more salient in dynamic trials and this is what was producing the effect found in the first study. By using the same stimuli outlined in the first study, participants were asked to rate both perceived emotion and attractiveness of either the dynamic faces or the static faces. It was found that (as expected) emotion ratings were more variable from the dynamic trial (supporting the notion that emotion is more readily available in dynamic trials) and that emotion and attractiveness were positively correlated. Static faces were generally perceived as neutral. It was concluded that the evaluation of static images is based on structural information as this is the only information available in a static face, and

that different evaluative methods are used when rating the attractiveness of dynamic faces as different characteristics are available, such as emotion. Such an investigation suggests the wealth of static facial studies investigating attractiveness do not tell the full story and that dynamic cues perhaps override structural characteristics when they are available to the observer.

Whilst this highlights the importance of motion in relation to human facial attractiveness, other more global movements of the whole body that should seemingly be more conspicuous (as the ability to discern expressions and emotion requires quite close contact) are still under researched in humans. However, as with most work regarding evolutionary principles, comparative literature provides relevant research relating to movement as a signalling mechanism in the realm of sexual selection. It is well documented that gait and certain specialised movements are viewed as courtship displays in which males signal both their interest and mate quality to observing females. In a recent review of the comparative literature, Byers, et al. (2010) stressed the importance of reliable indicators of genetic quality in a male, and noted that because of the absence of extreme ornaments in many mammals, females judge males based on their motor performance. The authors suggest that movement is in fact a better indicator of quality than static cues because it allows for the assessment of quality in a much more honest way thus reducing uncertainty in mating decisions. Vigour and skill are two features that are predicted to be particularly important aspects of male quality that are used by females in order to accurately gauge mate quality.

Vigour (or fitness) is an aspect of movement that cannot be faked and crucially is an expression of a male's full genome and captures a wealth of aspects of the organism including his ability to resist parasites and his immunocompetence. Several researchers have reported that females assess a male's genetic quality using vigour.

The second factor is that of motor skill. Whereas vigour is a general measure of physical fitness, skill involves precision and coordination which Byers et al. (2010) suggested is a better measure of genetic quality as it encompasses factors such as health, the musculoskeletal, nervous and sensory systems, as well as developmental stability. Displays of motor skill vary among species, and whilst in the past researchers have observed these displays and generally speculated they are selected for because they provide a reliable indicator of quality, Byers et al. (2010) argue that it is the skill of the movement that is of particular importance.

1.5.1 Courtship Displays in Practice: Spiders

Several researchers outline the curious vibrating and drumming displays some species of male spiders use to attract the attention of a female that are a clear example of vigour. Female wolf spiders (*Chizocosa lycosidae*) for example base their mate choice decisions on the frequency of body shakes and leg rises in males (Rypstra, et al., 2003). Hebets and Uetz (1999) report that male wolf spiders stridulate (produce vibratory sounds) their abdomen on dry leaves thus producing a drumming sound and is thought to be the key selective force in female choice. Kotiaho et al. (1996) experimentally induced this behaviour by creating mating environments in plastic boxes with dry birch leaf bases and observed female choice over several pairings. It was found that males who drummed with greater frequency (i.e. more vigorously) were selected by females for mating. This pattern of abdomen movement has also been extended to funnel-web spiders (*Agelenopsis Aperta)*; Singer et al. (2000) reported that males with greater frequency of abdominal swinging were much more likely to mate with a female.

Clark and Morjan (2001) describe different dynamic courtship displays in male jumping spiders (*Maeva inclemens*). The authors studied two varieties (or morphs) that mate with a common female, in order to investigate the effectiveness of different courtship displays. The authors noted that the two spiders display different courtship behaviours when trying to attract a female. The tufted morph starts by positioning himself around 9cm from the female and standing up and waving his front legs in the air vigorously and swaying his abdomen side to side. The grey morph stands closer to the female (around 3cm) and while in a prone position slides back and forth with his first two pairs of legs pointed forward in a triangle-like configuration. Both morphs are physically distinctive and use different motor displays as a way in which to attract the attention of the female. However both morphs share the same degree of success with regard to offspring. It is suggested that such species of spiders use courtship displays to attract the attention of the female as her preference for a mate is solely down to whichever she sees first.

1.5.2 Courtship Displays in Practice: Birds

Whilst spiders appear to be using vigour as a method of attracting attention of females in mating contexts, several species of bird demonstrate both vigour and skill alongside their vocal performances.

Many researchers have observed that birdsong production is selected for in many songbirds (Nowicki et al., 1998). From the outset, birdsong seems like an unlikely test of Byers et al.'s prediction on motor skill and vigour; however birdsong is a very close fit with motor skill. Nowicki et al. (1998) addressed the question of why birdsong seems to be selected for in many male birds by suggesting that the underlying mechanisms are indeed dependent on male condition. In order to sing, birds have to have intricate control of

breathing, syrinx and vocal tract modulations, i.e. birdsong relies on motor skill. A key aspect of birdsong is that it has a large learned component and depends on cultural transmission for its expression (Nowicki et al., 2002). Searcy et al. (1985) for example found that in male song sparrows (*Melospiza melodia),* a lack of song tuition leads to minimal response from females. Furthermore, male song sparrows deafened before they had the opportunity to learn a song repertoire received no female interest at all (Searcy & Marler, 1987). Nowicki et al., (2002) demonstrated that song learning is very important and females respond strongly for well learned species-typical songs. These studies demonstrate that whilst skill and ability may be very important factors, in complex culture-bound aspects of behaviour, learning how to utilise these abilities from peers is of equal importance.

Similar to the motor skills involved in singing, whole body dynamic courtship displays too rely heavily on many of the same underlying condition dependent systems. Williams (2001) investigated the song and display patterns of Zebra Finches (*Taeniopygia guttata)* and suggested that song accompanies plumage erection and ritualized locomotion. Williams stated that all birdsong by the finches was accompanied by dynamic performance.

More recent research investigating birdsong and courtship display has provided an interesting theory that might explain why song and dance are often closely related to one another as well as why some birds (particularly those who can vocally mimic sounds) can follow a rhythm. Both the African grey parrot (*Psittacus erithacus)* and sulphur-crested cockatoo (*Cacatua galerita eleanora*) are able to rhythmically move to a beat (auditory entrainment), a characteristic once assumed to only occur in humans (Patel, et al., 2009). It is thought that the trait of vocal mimicry is closely related to the ability to move in synchrony with a beat, as the brain mechanisms involved (the basal ganglia and supplementary motor areas) are related. Patel et al. predicted that such mechanisms evolved similarly in humans in that the ability to dance/move to a beat evolved as a by-product of a function that primarily

allows us to mimic sound (i.e. learning language). Schachner et al. (2009) investigated the hypothesis that auditory entrainment evolved as a by-product of vocal mimicry. The authors predicted that all species that sing or have a vocal mimicking ability should exhibit signs of an auditory entrainment capability. In order to investigate this, they presented a novel auditory beat stimulus to an African grey parrot and sulphur-crested cockatoo and found that during presentation, the two birds displayed head bobbing and foot lifting in time with the beat (neither had been trained to respond to acoustic material before). To further their support for the hypothesis, the authors conducted a video database search investigating whether non-mimicking species also had entrainment abilities. It was found that only mimicking species and humans possessed the ability of entrainment. Such evidence does suggest that entrainment is a by-product of vocal-mimicry and provides compelling evidence that both auditory entrainment (dancing) and movement are inextricably linked, and explains why dancing is often to a specific beat.

Of course not all birds sing but many perform courtship rituals much akin to dancing, and females attend to these displays to make mate choices. Several researchers have written about the often unusual motor displays that male birds make. For example Prum (1990) describes male manikins (*Aves pipridae*) as performing backward slides along branches by moving their feet incredibly quickly. Scholes (2008) also described courtship movements in birds of paradise (*Aves paradiseaeidae*) including horizontal perch pivots, head tilting, hops and charges, shakes, bouncing and 'ballerina' dances. Byers et al. (2010) hypothesised that birds with bright plumage (like the manikins and birds of paradise) have developed these motor skill displays as a secondary adaptation to enhance the visual stimulus of the plumage thereby increasing its visual impact.

In hummingbirds (*Calypte anna*) too, males perform dive and shuttle displays to protect territory from both other males and females attempting to steal his nectar supplies (Stiles, 1982). These seemingly aggressive displays also function as courtship displays incited by females, possibly to assess the male's ability to defend a territory. Stiles described a rather complex series of aggressive dives and back-and-forth shuttle displays accompanied by high intensity singing preceding copulation during the mating season. He concluded that these displays are used to assess potential mates and have evolved to be long and complex to aid the female's decisions. Clark (2009) further notes that these dive displays (both defensive and courtship related) hold the record for velocity attained by any vertebrate showing that just as females can generate extreme ornamentation in males, female mate choice may cause males to perform dynamic courtship displays at near intrinsic performance limits which would require peak physical quality to successfully perform. In other species, females have been found to prefer males who perform close to intrinsic limits of muscular and vocal abilities, which strongly suggest this is a way of assessing overall condition (Bostwick & Prum, 2003, 2005).

Finally, more recent research by Barske et al. (2011) also found that courtship motor displays by males were an important consideration for female golden-collard manikins (*Manacus vitellinus*). Males perform elaborate and acrobatic courtship displays on branches called 'jump-snap' displays. This involves jumping extremely quickly between saplings on branches and quickly producing snapping sounds with his wings; in between jumps he temporarily freezes and shows off his golden throat feathers, presumably to provide additional evidence of his quality. These displays are energetically costly to the male and require him to be in extremely good condition to perform these feats. Females observe multiple males before deciding which one to mate with, suggesting that these displays are indeed a form of assessment. Interestingly, Barkse et al. (2011) reported research that

indicates that the motor patterns evolved before morphological static traits such as plumage colour, suggesting that the latter evolved as secondary traits to further highlight the motor skills. To observe such feats, the authors deployed high-speed video cameras into bird habitats and recorded over the mating season. In addition to this, prior measurement of beard (golden chest plumage) and body weight as well as tagging took place. The authors found that females are extremely sensitive to such displays and can discern differences of only a few milliseconds and prefer (and preferentially mate with) males who are faster. Even small differences of tens of milliseconds profoundly impacts female preference. Furthermore, higher male heart-rates were indicative of female preference suggesting large metabolic investment in such displays. As a result the authors conclude that females are using such displays to assess cardiovascular function and overall condition.

In summary, it appears that birdsong and the accompanying visual displays have signalling capacities that indicate vigour and motor skill in birds; both cues are difficult to fake and may represent honest signals of male quality. In many birds, birdsong and its accompanying dynamic performance are primarily used as courtship behaviours and selection has likely acted in a way in which to indicate to a female a male's genetic condition. Møller (1990) previously indicated that findings in relation to static ornaments and features may not be as clear cut as once thought and other signals may be utilised by females in order to make an accurate judgement. More recently researchers such as Byers et al. (2010) and Barske (2011) suggest that assessment of movement displays may provide more easily accessible information about condition and that static cues serve to support such displays.

1.5.3 Courtship Displays in Practice: Mammals

Unlike birds, acrobatic movement displays are not commonly described in mammals but females are still thought to make mate choice decisions based on movement.

Research on ungulates has identified courtship display patterns that are thought to be involved in mate selection. Byers et al. (1997) observed the behaviour of pronghorn bison (*Antilocapra americana*) and like many ungulates, the most successful males are the ones who maintain the largest harems. This requires males to often defend their harem by chasing away other males, an activity that requires a great deal of physical energy and stamina (vigour) for the two week mating period, during which their rest and feeding time is dramatically reduced. These harem defences were not fights between males (in the typical intra-sexual sense) but are defined as tight herding behaviours performed by male bison in order to fend off other males and round up females. Byers et al. noted that it is quite common that females stop grazing and watch a male's performance in this task and those females only mated with harem-controlling males if the male successfully fended off non-harem holding males (Byers, 1994). Byers (1997) also observed a curious courtship display of the pronghorn that he termed the 'circle chase' which is thought to be used by females as an assessment of male vigour. In a circle chase, a male seemingly initiates the chase (however it is unknown if this is true or the male is simply reacting to subtle, possibly olfactory cues from the female) by rushing towards a female. The female then starts to run away (but not in an attempt to escape the male) and performs tight loops changing direction often and sharply whilst the male follows closely behind but does not attempt to close in on the female. After approximately 60 seconds the chase ends and the female returns to the harem.

Displays of agility and stamina in male ungulates have also been documented in both bison (*Bison bison)* (Lott, 2002) and bighorn sheep (*Ovis Canadensis)* (Hogg and Forbes, 1997). Lott described how female bison often run away from a male the moment he achieves

intercourse and males often remain on their hind legs until ejaculation. Similarly, an even more unconventional movement pattern, which is highly dependent on agility, strength and stamina, occurs in bighorn sheep: here males mate with a female as she runs, which requires extreme agility but proves to be quite successful (Byers et al., 2010).

1.5.4 Courtship Displays: Chimpanzees

Movement patterns in species such as birds are not necessarily representative of the origins of possible human courtship displays, as it has been shown that such displays are indicative of different aspects of condition. If dynamic courtship displays were used as an honest signal of human mate quality and did evolve through sexual selection in the way that species like spiders and birds have, then studies of our closest genetic relative, the chimpanzee could shed some light on the origin of dynamic displays in humans.

Chimpanzees (*Pan troglodytes)* have been shown to perform courtship movements. Lawick-Goodall (1968) in her review of chimpanzee behaviour in the Gombe Stream Reserve found that such movements were almost exclusive to males. The author outlined six separate behaviours that males perform to attract females: i) Bipedal swaggering – this is a form of courtship dance and includes firstly sitting or standing bipedally close to a female, extension of the hands and the releasing of the head while stepping side to side. ii) The sitting hunch – a typical courtship display seen predominantly in adolescent males. iii) Branching – the male may branch his arms out to the female. This is often accompanied by swaggering. iv) Glaring – more dominant males were observed being able to simply glare at a female to make them approach and copulate. v) Beckoning – the male sits in a bipedal stance and raises his arm above his head and makes sweeping motions toward her. vi) Tree leaping – when both the

male and female are in a tree, the male may swing from branch to branch and perform leaps in a rhythmic fashion. He executes this while looking at the female. Lawick-Goodall noted that females positively responded to 82% of the above displays if displayed by a more mature male, however if the male was adolescent, response dropped to a rate of 77%. Whether or not the movement itself is in any way related to maturity and thus an honest cue of maturity remains to be seen. The bipedal display (or swagger) has been found to occur in most male chimpanzees in only three contexts; courtship, charging display and frustration (Kuroda, 1984). Kuroda (1984) also noted that females do not receive any other visual sign of courtship other than the dance itself.

1.5.5 Summary

Comparative research has outlined that in many species, males perform complex dynamic courtship displays, often at the very limits of their abilities, whilst being observed by females. Much of this research has suggested that such displays have developed for the purposes of mate choice as a form of honest signal that are impossible to fake. Byers et al. (2010) outlined two common facets of these courtship displays: vigour and skill. Vigour is heavily reliant on physical fitness, strength and endurance whilst skill additionally requires precise motor control, which utilises the musculoskeletal and central nervous systems. Many studies report that females indeed prefer males with the most spectacular and vigorous displays although none have reported whether or not these males have greater reproductive success.

1.6. Basics of Human Movement Perception

In humans, research to date is just beginning to consider the potential signalling capacities of movement in relation to sexual selection. However, perceptual research has long considered this avenue of study. The ability to detect motion in general is an ancient information channel (Troje, 2003) and is often a critical sense important to the survival of an organism as the ability to accurately perceive motion can be the difference between life and death (for example communicating and understanding cues from conspecifics of a threat in the area). In addition, the ability to detect, track and hunt prey is another example of the usefulness of accurate motion perception (Saygin, et al., 2004). In evolutionary terms, if motion detection did evolve as a result of natural selection, then the ability to accurately identify other species (i.e. threats) rather than being confined to conspecifics would also be of benefit to survival. Mather and West (1993) investigated whether humans are only proficient at perceiving human dynamic cues or if they can discriminate between different species based on movement alone and found that participants were indeed able to accurately discriminate between different animals based solely on dynamic cues, thus giving credence to the hypothesis.

Research has also pointed out that motion detection (particularly that of biological motion, a term commonly used to describe the movement in organisms) is either innate or develops extremely quickly. Vallortigara, et al. (2005) found that newly hatched chicks showed preference for biological motion stimuli rather than rigid, non-biological moving stimuli, suggesting that there is an innate mechanism for the detection and preferential gaze for biological motion. This also extends to humans, infants only 12 weeks old can accurately discriminate between upright and inverted walking motions (Berthnthal, et al., 1987), and this ability is fully developed by eight months of age (Hirai & Hiraki, 2005).

In addition to detecting possible threats, humans use motion detection to gain information on each other in social contexts via actions they perform every day for example; deriving people's intentions and signalling to one another non-verbally using gestures in response (Grossman et al., 2005). In addition, humans can use movement to identify people we know solely using movement cues in the absence of other visual signals, for example in low light and in crowded areas (Cutting & Kozlowski, 1977). Furthermore, it is even possible to detect emotions and personality traits via such cues (Brooks et al., 2008; Blake & Shiffrar., 2007).

1.6.1 Brain Reigons Involved in biological motion perception

Due to the survival benefits and the usefulness of accurate motion perception in our highly social world, we have developed specialised structures and neural circuitry that allow us to make decisions based on movement very quickly, often without conscious awareness. Two theories attempt to explain this rather extraordinary ability to detect biological motion, especially that of other human beings. The first theory suggests that our increased sensitivity to human movement is because of a link between the vision and action centres of the brain for example, our own movements may facilitate the movement we see (Prinz, 1997). The second theory simply stipulates that because we see so much human movement, it increases our sensitivity (Johansson, 1973; Jacobs, Pinto & Shiffrar, 2004).

The neural network specific to biological motion perception has been the subject of much research and many researchers have begun to map out these areas using both healthy and clinical brain trauma patients.

Signals from the eye travel down the optic nerve to the occipital lobe for processing. Starting in the visual cortex (V1), visual information it is then transmitted to a variety of areas for more specific processing. A two-pathway theory by Ungerleider and Mishkin (1982) proposed that visual information was transmitted by the dorsal and ventral pathways (known colloquially as the *where* and *what* pathways respectively). Since then it has been argued that this was too simplistic an approach and the perceptual system is in fact intertwined with many other structure and areas of the brain that is beyond the scope of this overview (for example Ungerleider & Haxby, 1994; Milner & Goodale, 2008).

Beyond initial visual processing, several specific areas have been identified in the perception of biological motion in particular. Beauchamp, et al (2002) noted that several primate and human studies have identified that the middle temporal (MT) visual area (sometimes referred to as V5, an area on the border of the occipital and temporal lobes) responds to moving stimuli (be it biological or not; Bonda et al., 1996). In addition to this, anterior and superior to MT/V5 is the superior temporal sulcus (STS), a region that appears to respond to biological motion such as hand, eye, mouth and body movements (Allison et al., 2000). It is also thought to be the site of synthesis for the dorsal and ventral streams (Vaina et al., 2001). Beauchamp and colleagues set out to tease apart whether the same regions of the brain were activated when participants were shown pure biological movement, or the motions of tools (whose motion is derived from human movement). Previously it had been noted that pictures of tools elicited activation of the middle temporal gyrus (MTG) in the temporal lobe, whilst pictures not associated with human movements did not. Utilising the functional magnetic resonance imaging (fMRI) technique, 18 participants were shown either full body motion (depicting many actions) or videos of tools being used. It was found that whole body biological motion elicited strong activations of the STS whilst tool motions activated the MTG.

More specifically Grossman, et al., (2005) conducted a repetitive transcranial magnetic stimulation (rTMS) experiment to investigate which regions of the brain were responsible for the perception of biological motion in healthy volunteers. This technology involves a magnetic coil being located on places of interest on a person's skull, and the equipment either hyperpolarises or depolarises underlying neurons using a rapidly changing weak magnetic field. The aim of the technique is to either elicit responses in specific brain regions or inhibit (interfere with) them. Grossman notes that patient groups with damage to the STS have difficulty discriminating biological motion from non-biological motion. However such patient groups are still able to perceive lower-level motion processing such as detecting speed and tracking as this is handled by area MT/V5 (Bonda et al., 1996), earlier on in the processing pathway. Using nine healthy volunteers, the authors temporarily disrupted the functioning of the STS or area MT+/V5 and presented participants with animations of actions such as walking, running and kicking. It was found that disruption to just the right hemisphere posterior superior temporal sulcus (referred to as pSTS) was sufficient to impair recognition and discrimination of biological motion perception from non-biological motion. Disruption to area MT/V5 however did not have any effect on participant's performance.

Another strand of evidence for the involvement of the STS in biological motion processing is from lesion and brain damage case studies whereby parts of the visual processing areas have been damaged. This allows researchers to link patient behavioural deficits with damage to specific brain regions. It has been found that even if more basic visual processing pathways and structures have damage, participants still have the ability to discriminate biological motion. Vaina et al. (2001) reported findings involving lesion patients such as AF who sustained injuries to the ventral pathways, including area MT/V5 but not the STS. Due to the MT/V5 damage, AF was classified as 'motion blind' but could still easily recognise human actions depicted in point light displays. Vaina et al. however noted that

patients with damage to the STS were unable to recognise the most simple biological motion displays, but could still perceive object motion. In healthy participants, brain activation (assessed via fMRI) was observed in the right hemisphere pSTS when point-light biological motion was viewed, as well as when sequences of mouth and eye movements were seen. Interestingly, although it is tempting to associate biological motion to primarily the dorsal pathway, activation of both the dorsal and ventral pathways was observed during presentation of biological movement, suggesting that both *what* and *where* pathways converge here to provide such information. Furthermore, the cerebellum was also activated during motion presentations..

As identifying the intention and other higher-order information from human biological movement can be seen as a social process, some research has attempted to link the amygdala, a brain region strongly implicated in the processing of emotion, to the viewing of biological motion. Bonda et al. (1996) conducted positron emission tomography (PET) to measure blood flow in the brain whilst participants viewed animations of either the frontal view of someone dancing, an arm/hand reaching out and grasping a glass, or a geometrical object that moved around. As expected, it was found that the pSTS was activated during the body movement and hand grasping sequences. In addition to this, significant differences were observed in amygdala activation between the body movement condition and the non-biological movement condition, suggesting an emotional response was triggered whilst viewing full body motion. From a social context this makes sense as we constantly make emotional connections with other people, and this finding demonstrates that this occurs even from the known motion of a human being.

Other researchers have confirmed the activation of the amygdala and other structures involved in emotion processing during presentation of body movements in fMRI studies.

Gelder, et al., (2004) investigated the perception of fearful movements that were videotaped using semi-professional actors. The authors found that participants presented with whole body fearful movements produced higher activity in such emotion-related areas (right amygdala, orbitofrontal cortex, posterior cingulate, anterior insula, nucleus accumbens and retrosplenial cortex). In addition to this, when fear expressions were viewed areas in the motor cortex were also activated. Such evidence suggests that when viewing emotionally charged fearful expressions in the whole body, the fight or flight response was initiated.

Finally, researchers have attempted to link biological motion perception areas with the pre-motor cortex in the frontal lobe. Previous research has identified that action perception activates such cortical areas using 'mirror neurons' that fire on action production as well as action perception, and are using information from their own representations of such movements when perceiving and understanding the actions of others (Saygin et al., 2004). Saygin et al. (2004) investigated whether or not human biological movement was sufficient to activate the frontal cortex in this context. Using fMRI they found this to be the case with the right hemisphere pSTS being activated in the same pattern of the frontal areas of the inferior and precentral sulci, areas known to be important in action observation. It was concluded that in order to accurately perceive the actions of others, one must actively fill in the gaps using information from our own motor system thus supporting the notion of mirror neurons.

In summary, it appears that there is a distinct activation of the right hemisphere posterior STS when viewing biological movement. It has been proposed that although this appears to be the centre for biological motion processing (where the ventral and dorsal visual pathways integrate), the brain utilises several other areas in order to accurately fill in the gaps such as spatial integration (cerebellum) and action perception (pre-motor cortex) as well as the emotional circuit (amygdala) from very sparse visual information such as a selection of

light points attached to a person walking thus indicating that movement is an integral cues to social perception.

1.6.2 Methodology of Motion Perception and Person Identification

In order to investigate motion perception in an empirical way, a methodology that eliminates as many cues that could confound or influence people's perceptions is required. For example, if judging the whether someone is male from a regular video clip, observers can use static cues of the face, height and build in order to base such judgements. Lippa (1983) investigated static absolutes (such as height and weight) and relative (shape) cues people use to judge the sex of an individual. Lippa (1983) outlined twenty-four bodies and asked eighty-six participants to judge whether the outline was male or female as well as whether they perceived the outline to be masculine or feminine. It was found that the most important features of the body used to judge sex accurately were waist and shoulder width. Lippa (1983) concluded that the "*waistedness of the body outline was a dominant cue to the gender*" (p. 673). This poses an inherent problem of how to eliminate static cues whilst maintaining the pertinent movement information. Bente et al. (1996) suggested that the majority of investigations into non-verbal behaviour have had to accept the confound of static traits such as attractiveness and body shape because such cues are impossible to control for, as even getting different actors to do the same task, inherently yields different results.

To combat these issues, methods have been developed that isolate only the most pertinent cues of interest. A large body of research has focused on the motion cues necessary in order to make accurate judgments of an individual's sex and it appears that movement indeed plays a large role. Methods that mostly control for the aforementioned confounds have

actually been available as far back as the late 1800's. Jules Marey (~1880, reported in Dagognet, 1992) was able to develop a high-speed photographic technique whereby many different photographs could fit onto a single plate. This was called 'chronophotography', and in order to emphasise dynamic information' Marey placed markers on the major joints of a black-suited person and filmed them walking. The biggest issue however, was the quality of the images produced; due to the high-speed technique, the quality of the image was significantly degraded. It was not until the 1970's when Johansson (1973) adopted Marey's principal, but applied more modern imaging hardware. Johansson's (1973) aim was to produce a reliable method to exclude confounding information whilst keeping the dynamic biological motion pertinent. He achieved this by dressing participants in black clothing (head to toe) and attached light bulbs to the shoulder, wrist, elbow, ankle, knee and hip joints. He then darkened the room and filmed the participant using a standard video camera. This provided very smooth, 2-dimensional animation. An early criticism of the said method was that background markers could become occluded if markers in the foreground passed in front of them. Johansson (1973) placed some reflective ribbon on the markers that overcame this problem. When he showed clips to observers, he turned the contrast of the video up to maximum and reduced the brightness to minimum in order to emphasize the points on the screen rather than the remnants of the structure of the actor. He demonstrated that even with very sparse cues (only 10 markers presented for 1 second) that all observers identified that the clip was of a walking man. In a subsequent experiment he demonstrated that observers had no trouble identifying various other activities via so-called "point-light" stimuli such as running, dancing, cycling, painting and press-ups. A further discovery was that if the animation stopped, participants were not able to identify the marker outline as a human body thus showing that motion was of key importance to person perception.

Later, Kozlowski and Cutting (1977) addressed a key question on whether people could perceive the sex of a walker purely from their movements. Using a variant of Johansson‘s (1973) methodology, three men and three women walked up and down a straight line until the researchers were happy they were not deliberately altering their gait in the knowledge they were being filmed. Filming was done from the sagittal view, approximately eight metres from the walkers and participants had reflective tape around their ankles and small patches on the other joints. The authors randomised sixty trials (six walkers, ten times each) and displayed them to thirty undergraduate students (fifteen men, fifteen women). Results indicated that correct identification occurred around 70% of the time but only after one female walker was omitted. Other results include that best identification occurred when the whole body was presented, but observers still performed significantly above chance level when viewing the upper body alone. When participants were asked which parts of the movement they thought were male and female, 76% of participants identified shoulder sway as indicating maleness and 100% of participants attributed hip movements to females. Curiously, in a subsequent experiment the authors demonstrated (albeit with a reduced sample size of two male and one female walker) sex identification was possible from just the ankles alone, although to only slightly above chance at 54% (however still significant).

The authors later presented additional data (Kozlowski and Cutting, 1978) that added additional walkers and rater’s in an attempt to boost power, and concluded that sex identification from ankle movements alone was quite poor, suggesting that more global cues in the full displays are more pertinent for the perception of gender. Barclay et al. (1978) then investigated the necessary display time a person needed in order to accurately assign gender to point light walkers, and found that participants needed more time to make this decision than to simply perceive the stimulus as a human walker (which was around 200ms in Johansson, 1973), around 4.4 seconds. In addition to this Barclay et al. conducted a number

of other experiments to assess conditions in which sex identification was impaired. They found that observers could not accurately sex a walker if the presentation rate was slowed, nor if points were aggregated into a single mass. The authors also considered that a dominant cue to sex identification was walking speed and stride length, however participants were still accurate above chance even when these were controlled for.

Interestingly, if standard point light displays were inverted (showing point-light displays upside down), performance dropped to significantly below chance, an effect reminiscent of inversion effects in faces (Farah et al., 1995) (i.e. if an upright walker was correctly perceived as male, the same display inverted was reported as being female). The authors (with some caution) speculated that this inversion impedance may be due to the difference in structural sway of the shoulders and hips. Males have broader shoulders and females have wider hips (this is reflected in their sample) and these differences cause body segments to sway more. The inversion effect reverses the position of the points on these structures deceiving people into thinking that shoulders are hips and the hips are shoulders. Bertenthal and Pinto (1994) however suggested that it was unlikely that observers are using rigid relational cues (i.e. rigid relations between two or more joints, shape) or individual movements of single point-lights as these were similarly present in inverted stimuli. The authors conclude that participants use global cues to perceive biological motion, and when these are inverted, the form becomes less human in appearance because we have a stored, orientation-specific representation of the human form, this is violated when the walker is inverted thus creating the ambiguity.

Several researchers have since replicated the sex identification finding as well as extended it to recognition of specific people and themselves. Cutting and Kozlowski (1977) demonstrated that by using sagittal-view point-light animations, participants performed quite

well when trying to recognise friends, often scoring above chance level (63%). Upon asking participants how they came to such judgements, participants who were particularly adept at the task were typically found to be using dynamic cues such as the bounce of the walk, arm swing or speed; whereas participants who performed poorly at the identification task used static cues such as height. In addition, Beardsworth and Buckner (1981) conducted a replication and found similar results in the accuracy of identifying friends. There was however an unusual advantage of participants being better able to recognise themselves than their friends. This is something of an anomaly as humans typically do not see themselves moving (unless looking in a mirror) (Loula et al., 2005).

One of the most informative papers was that of Runeson and Frykholm (1983) who commented upon six different biological motion experiments. They discovered several effects; firstly that participants viewing a person throwing an object (a sandbag) that is invisible (i.e. the person is represented using the point light-technique and the thrown object is not marked) can accurately perceive the length of the person's throw. Secondly, participants' lead-up movements to the lifting of an invisible object can produce accurate judgements of how heavy the lifter perceives the object to be. Thirdly, a lifter cannot deceive participants into the thinking the box is heavier or lighter than it actually is. Finally, the authors investigated gender identification, and criticised Cutting and Kozlowski (1977) for allowing participants more than one judgement of a point-light walker, claiming that participants may have produced a high consistency rate due to the fact they may have recognised the point-light walkers from previous trials due to "idiosyncratic gestures or irregularities in the placement of reflectors" (p. 604). Runeson and Frykholm (1983) also increased the amount of point-light walkers from 6 (as in Cutting & Kozlowski's study) to 20, half of whom were adults and half were prepubescent children in an attempt to eliminate the height of a point-light walker as a confound. Instead of just walking, participants were

asked to perform several tasks from walking and running, lifting boxes, throwing blackboard erasers and sitting down on a chair. This produced a varied video of typical tasks that one might observe a stranger engaging in. Performance was relatively good on the task, averaging 75% correct identifications of gender with more correct responses for adult men and young girls.

Further to the original gender study, Runeson and Frykholm (1983) investigated whether a person could actively deceive an observer into believing they were viewing a member of the opposite sex. Actors were asked to perform similar actions to those outlined in the original gender experiment and either not told about gender to prevent self awareness, over emphasise their own gender (i.e. act stereotypically) or try and act like the opposite sex in the way they moved. Overall gender identification was correct in 85% of cases in the natural condition (no deception) however accurate judgements were only slightly lower for the full deception group (i.e. participants accurately judged the real sex of the actor despite deception). This suggests that dynamic cues (even if the person is attempting to fake them) can honestly signal the sex of a person.

Berry et al., (1991) devised an alternative method and attempted to replicate some of the findings of Runeson and Frykholm (1983) (particularly that of gender recognition and attempting to deceive observers using movement) claiming that point-light methodologies were very obtrusive to participants, making them feel more self-conscious having reflective markers placed onto their bodies, that could then be influencing their subsequent movements. To control for this, the authors employed a regular filming technique whereby participants did not require special attachments to their bodies. To obscure static features, the resulting video clip was ‘quantized’ thus creating a mosaic style blur by reducing each frame into a series of 16x16 pixel blocks and each pixel in each block was standardised in colour and luminescence to the mean colour of that block. The resulting clip obscured static structural

information but viewers were able to see the movement, as the mean light in each block changed according to the actor's position in the scene (i.e. as the actor passed through the blocks the mean colour hue would change). Using such a technique observers were able to accurately determine sex of a participant from the dynamic quantized display. However sex recognition was less accurate than recognition from point-light displays suggesting that point-light displays may be clearer and easier to process.

Although the above methods are able to eliminate certain static confounds (such as physical attractiveness), their reduction of biological motion to just a pattern of dots is not ideal, as this is not representative of the way we see people in the natural word. Furthermore, due to the technological constraints at the time, the resolution of the presented stimuli was low, and often relied upon degrading stimuli to eliminate familiarity cues that in turn affected overall quality. Furthermore, although using point-light animations eliminates some possible confounds, important factors such as height and build are not fully controlled for because the markers are placed directly on the individual. Finally, many of the aforementioned studies recorded walking from a sagittal view which minimises the emphasis of important aspects of shoulder and hip sway (most likely to control for the different widths in males and females). It is possible that even more accuracy in sex identification and additional higher-order information might be present when stimuli are presented at different angles.

Advances in technology over the past ten years have allowed researchers to remedy some shortfalls in the basic point-light method. Modern motion capture systems utilise multiple high speed, specialist infrared cameras to capture reflective markers (PL) in 3 dimensions at high resolutions. They have introduced the ability to extract accurate biomechanical joint kinematics for analysis. Moreover, researchers can now realistically manipulate variables such as height and build in point-light displays to exert control over their stimuli by mathematically aggregating several optical markers.

Researchers such as Troje (2003) have adopted such systems and applied them to perception research. Firstly, in order to validate such hardware, replications of previously robust findings in sex discrimination have been conducted. Troje (2003) found that correct sex classification occurred in 75% of cases and discovered that identification was optimal when the point light walker was presented in frontal view. Previous research by Cutting and Kozlowski (1977) revealed correct gender identification in only 63% of cases, only 13% above chance; that, Troje argued, was due to the sagittal viewpoint utilised in those studies. It has been suggested that the frontal view is the most informative because many diagnostic cues are only visible from the front Pollick et al., (2005). The most pertinent cues were found to be hip sway in females, similar to that of a catwalk model; a rather slim frame, elbows held close to the body, the upper body displaying very little movement and feet placed one foot in front of one another. In contrast, a stereotypical male movement is characterised by large lateral shoulder sway, typical of a western hero's walk; straddled legs and elbows that are held away from the body with little hip movement.

In order to gain better insight into the visual system's use of motion cues, researchers have manipulated and scrambled point light displays to investigate the cues necessary to accurately perceive a variety of attributes. Several researchers have investigated the effects of inversion on perception of walking direction using a 3D motion capture system (Troje & Westhoff, 2006; Chang & Troje, 2009; Hirai et al., 2011). It had previously been noted that inversion inhibits accurate perception of walking direction (Bertenthal & Pinto, 1994), similar to the deficits seen in gender recognition by Barclay et al. (1978). Barclay suggested that this might be due to local point-lights of the hips and shoulders being swapped that were confusing observers. Bertenthal and Pinto (1994) suggested that this may in fact be an effect of a stored holistic representation of an upright walker becoming invalid when stimuli were inverted. By scrambling the motion vectors for each point-light (thus eliminating the

structural cues), participants in all three studies (Troje & Westhoff, 2006; Chang & Troje, 2009; Hirai et al., 2011) were still able to discern walking direction based on the foot marker acceleration. This suggests that walking/facing direction at least determined via local point-light information given in the feet markers. No recent research to date has addressed the question of whether sex information is derived from a holistic point-light animation or from local point lights, although it seems logical given the evidence from Bertenthal and Pinto (1994) that we perceive sex through biological motion in a more holistic manner.

A further novel finding with modern 3D motion capture methods is that in the identification of sex, people who are perceived as having a female walk appear to be walking away from observers and people perceived as having a male walk appear to be walking towards the observer. Brookes et al. (2008) speculate that this could have evolved as a mechanism that "weighs the possible cost of misinterpreting the actions of others" (p. 729). For example, as males are typically seen as the more dangerous sex, the perceptual system has evolved to make it always appear like a male is travelling towards you as a safeguard to prepare the observer for fight or flight.

1.6.3 Perception of emotion from motion cues

Aside from merely recognising the sex of people from their walks or the ability to recognise friends and oneself, other researchers have discovered that social characteristics such as emotion appear to be encoded into human biological motion. Everyday movements may not consciously be communicative, however, experience dictates that many of them carry messages (Bull, 2001; Pollick et al., 2001). By using day to day actions of the arm (knocking on a door and drinking), Pollick and colleagues utilised modern, 3D motion capture recording

equipment to record two actors performing these two actions with ten affects (afraid, angry, excited, happy, neutral, relaxed, sad, strong, tired and weak) following the reading of a brief story (although details of the story were not given). The authors then showed 14 undergraduate students the point-light recordings of just the arm movements from sagittal view and asked to name the affect from a list at the bottom of the computer screen. Participants were also presented with inverted and scrambled variants of these movements. It was initially found that many of these affects were misidentified, prompting the authors to further analyse only the key emotions of afraid, angry, happy, neutral and sad in knocking movements. By using these basic emotions, recognition rose to 59% for point-light and 71% for full video. Viewing the scrambled, inverted displays resulted in poor performance (14%) although more than half of participants recalled seeing human movement from such displays. This indicates that based solely on point-light arm movement's participants could recognise several key emotions. However, more global dynamic cues (rather than just the arm motion) may be required for more robust assessments.

Using a more basic methodology, Atkinson et al. (2004) investigated emotion perception form biological motion. Unlike using modern motion capture methods as in Pollick et al. (2001) and Troje (2003), the authors of this study used a technique very similar to Johansson's (1973) method of filming participants using standard equipment but covering them in reflective tape over selected clothing. Ten actors were instructed to portray happiness, sadness, fear, anger and disgust in a large room that represented the motion capture space in typical, exaggerated and extremely exaggerated forms. Thirty-six students then rated the variants of the stimuli (point-light dynamic, point-light stills (non-animated), full video dynamic, full video still) and it was found that (as expected) performance was best in the full video dynamic conditions, followed closely by point-light dynamic stimuli. Both

still conditions yielded quite good results although were typically around 20% poorer than point-light dynamic displays.

Perception of emotion is also readily observed when viewing point-light dance movements portrayed by semi-professional dancers (Brownlow & Dixon, 1997). Using a basic point-light methodology akin to Johansson (1973) and Atkinson et al. (2004), observers were able to very accurately judge happy from sad dancers. Sad movements were characterised as non-energetic, slow, sweeping movements and in contrast, happy movements were snappy, energetic and exaggerated. Dittrich et al. (1996) reported a more detailed experiment, using this same methodology (albeit using a higher resolution recording device and monitor) in comparison to standard video clips. Two experienced dancers (one male, one female) were recorded portraying a series of emotions (fear, anger, grief, joy, surprise and disgust) using both point-light (upright and inverted) and standard recording techniques. Seventy-two participants (36 male) then watched clips of the dancers and guessed which emotion the dancers were portraying. It was found that emotion recognition dropped from 88% in the standard video recording condition to 63% in the point-light animated condition (although still significantly above chance). Performance was near chance when viewing inverted point-light animations suggesting that emotion can be recognized when structural cues are missing but not when the global representation of a moving person is violated (inverted).

The conditions necessary for accurate emotion perception using biological motion cues were later examined by Clarke et al. (2005). Unlike other biological motion studies, these authors examined perception using interactions between two actors instructed to express sadness, anger, disgust, fear and romantic love. Participants were shown many configurations of these stimuli including upright and inverted versions of both actors together, single actors, and single actors which were mirrored. It was found that emotion

identification was good across presentation method for upright stimuli (apart from disgust which was often misinterpreted as other negative traits like anger or fear) and degraded when they were inverted or mirrored. In addition the emotions of romantic love and joy were impaired when they were presented without the other party. A final thought however, is that these two studies employed trained actors meaning inferences as to whether this emotional information is honestly signalled without training cannot be concluded.

It is also thought that many of these perceptual abilities to decode emotion cues from biological movement form a foundation to many other abilities such as the ability to communicate using body language, perceive intentions, and help construct appropriate responses to such communication (Grossman, et al., 2005). Kramer et al. (2010) used point-light animations derived from actual videos of two American presidential candidates to assess voting behaviour from the movements of politicians in a debate. It was found that ratings of perceived health from point light animations were the best predictor of voting behaviour suggesting that movement are providing information to people which directly influences decisions.

A final question is can ordinary (walking for example) movements be perceived as attractive, and if so what is mediating such attractiveness? Static cue research such as in face perception has suggested that PT exposure plays a significant mediating role in the development of structural characteristics such as jaw shape. Following this supposition, researchers such as Provost et al. (2008) hypothesised that the same process crafts the differences in the walking kinematics of men and women. By manipulating the masculinity of the point-light walk (i.e. altering the shoulder sway), they created a continuum of different walks. They then asked heterosexual women in the fertile phase of their menstrual cycle and women in the non-fertile phase to rate each walk on attractiveness. The women in their fertile phase rated the highly masculine walk as more attractive, suggesting that the way a man

walks may be indicative of some intersexual quality to women. Although tempting to conclude that this demonstrates that walking movements convey condition dependent information (i.e. possible PT based characteristics), the authors did not specifically measure any condition-dependent traits from male walkers as they artificially altered the gait.

1.6.4 Summary of methodology and future directions

Overall, the above research demonstrates that by reducing human biological movement to temporal cues, recognition of gender, intention, and emotion is still accurate, even with very short presentation times suggesting that movement is a powerful cue in many socially salient situations. Furthermore, research has suggested that movement is very difficult to fake even when people try and deceive observers and that it is possible that condition dependent cues can be detected from everyday movements such as walking (e.g. Provost et al., 2008).

However, despite attempts to make stimuli move naturally whilst eliminating static parameters, this commonly results in highly impoverished/basic stimuli for the people who view them that lack realism. Furthermore, a common criticism of the methodologies of researchers such as Johansson (1973), Cutting, (1978), and Berry et al. (1991) is that the stimuli are presented in 2D because only one camera is used from a fixed angle. In reality, our world is 3-dimensional and whilst recent advances in motion-capture equipment have allowed for 3D motion capture, research to date (for example Troje, 2003; Brooks et al., 2008) has only presented such stimuli in point-light form. This remains quite simplistic, and whilst this may be acceptable for the observation of simple movements such as walking, other, more complex actions may be more difficult to interpret.

Using a modern 3D methodology to investigate possible courtship displays in humans and presenting them in a point-light format may make stimuli overly simplistic and not sufficient to capture more elaborate movements (for example the emotive movements described in Brownlow & Dixon, 1997; Dittrich et al., 1996). It is possible however, to use such systems to record movements with great accuracy and apply a 3D avatar (virtual person) over the point-lights to create a realistic human form that controls for height and build. Using this approach would allow for a much better presentation method whilst keeping the empirical advantages of modern motion capture systems such as outputting biomechanical kinematics for quantitative analysis. This particular approach however has not been fully utilised in research to date and will form the basis of chapter 2 in this thesis.

1.7. Human dynamic cues of condition

Evolutionary research in humans has closely mirrored the investigations of comparative researchers, especially with regard to mate choice decisions. Despite this, research concerning the possible signalling capacity of human movements in relation to mate choice and sexual selection is still lacking despite this being pointed out over ten years ago (Farnell, 1999). Like mammals, humans do not possess vibrant plumage or extreme ornamentation; this makes static, visual cues such as fluctuating asymmetry and testosterone-dependent facial features difficult to discern, especially in low light or at a distance. The comparative literature cited above documents that courtship displays are intentional, often vigorous and require high degrees of movement precision (skill), which had led some researchers to suggest that dance most closely fits this context in humans.

1.7.1 Dance.

Dance is a universal human behaviour that can be traced back to cave art more than 20,000 years ago (Appenzeller, 1998) although this is a conservative estimate with some reporting that it may in fact be as old as bipedal walking (circa 2.5 million years ago) (Brown et al., 2006). Studying dance from an anthropological viewpoint had received relatively little research until 1960 when a paper by Kurath (1960) aimed to remedy the gap in the literature and kick start its investigation. Unfortunately this did not have the desired effect and only a few vaguely relevant papers were released in the following 15 years. An influential paper by Kaeppler (1978) provided a much-needed overview of the current standing of the dance anthropology and provided a much needed definition of dance as:

> "*a cultural form that results from creative processes which manipulate human bodies in time and space. The cultural form produced though transient, has structured content, is a visual manifestation of social relations, and may be the subject of an elaborate aesthetic system*" p. 232.

A further characteristic of dance is that it is almost always accompanied by music and/or an external rhythm or beat and being able to keep time to a beat is something that is thought to be almost exclusive to humans (Brown et al., 2006), although some studies have discovered vocally entrained birds of paradise also have this ability (Patel et al., 2009). Until Kaeppler's overview, anthropologists had relegated human dance as a very minor aspect to human behaviour rather than the key culturally defining, ritualistic, universal language it actually is. Kaeppler's review highlighted that the majority of studies into dance has concerned learning the styles of dance within different cultures, and it was clear that dance is highly dependent on cultural forms, but the paper did not speculate as to the meaning of dance.

This was later addressed by Hanna (2010) who argued that despite dance being diverse both inter- and intra-culturally, a common meaning or topic was being communicated; that of sexuality, gender and identity, as well as often having a large degree

of flirtatiousness. It was also noted that the main emphasis in many dance forms centres on the secondary sexual characteristics of the pelvis, breasts and hips in women, perhaps conveying information about fertility.

One of the key characteristics of dance is that it is considered aesthetically beautiful. Hanna (2010) explains that like modelling, dance allows for observation of the dancer for pleasure rather than any other function. A quote from Byers et al. (2010) supports this supposition:

> *"Almost every adult human can run a short distance, leap in a forward arc, land on one foot, and continue running. However, only a few adults, who we call dancers, can execute this motion in a way that we perceive as beautiful. Additionally, humans easily perceive performance differences between professional dancers, the actions of which must be nearly identical"* p 773

Such descriptions lend themselves to the hypothesis of dance being a form of ornament or courtship display as it shares similar definitions and intentions to dynamic courtship displays described in the animal literature. Like much of the courtship displays in the animal kingdom, dance is performed in the presence of others and is often an accompaniment to marriage ceremonies and other sexual contexts (Hannah, 2010). For example, lap dancing clubs (Miller, 2007) and nightclubs which are thought to function as human versions of animal leks (Hendrie, 2009) are often places people dance, especially with the opposite sex. Despite seemingly obvious links to the expression of sexuality and fertility, dance was not investigated in relation to sexual selection until relatively recently (~2005). In fact, Farnell (1999) had criticised the lack of research into the use of movement in general to questions regarding evolutionary theory, a fact that in comparison to the wealth of information on static cues to mate quality over the last decade still stands.

1.7.2 Human dance in relation to sexual selection

From 2005, dance had begun to be recognised as a possible cue to sexually desired traits, particularly in men. Brown et al. (2005) investigated whether the dances of 183 young people from Jamaica revealed information about their developmental stability. Fluctuating asymmetry was selected as the measure of developmental stability with nine traits being measured (elbow, wrist, knee, ankle, foot, third digit, fourth digit and ears) and for accuracy over time, each dancer was measured for FA twice, once in 1996 and then again in 2002.

Participants were asked to dance for one minute under constant conditions in a small area ($4m^2$) using an eight-camera Vicon optical 3D motion capture system, tracking a custom 41 optical marker set. The resulting point-light animations were then converted into basic humanoid figures whereby each body segment was represented by an ellipse. The authors chose 40 such dance animations (20 high FA and 20 low FA with equal male/female splits) and showed them to 155 young adults (87 male, 68 female) for rating on dance quality via a visual analogue scale. Independent of BMI and age, symmetrical males were rated as being better dancers, more so than asymmetrical males and symmetrical females. However the authors did not provide any conclusion as to whether they thought dance is used to make mate choice decisions, or why the ability to discern such information from dance movements may have evolved.

The Brown et al. (2005) study was among one of the first to explore sexual selection using dynamic cues and one which utilised a very robust way of recording such stimuli. However, Trivers, a co-author on the Brown et al. paper later revealed in Trivers et al. (2009) that the results of the study were almost completely artificial and that a large degree of the data was tampered with to ensure strong associations in the desired direction. A reanalysis of the data revealed at best extremely weak correlations between symmetry and dance quality.

As a result, evidence for honest cues to mate quality cannot be made from this research. Nevertheless, their rationale is well supported from the numerous animal studies into dynamic courtship displays and their methodology provides excellent control of structural cues whilst keeping motion pertinent.

Before evidence of fraudulent results in Brown et al. (2005), the authors did not speculate as to why or how dance may display such information. Fink et al. (2007) suggested that male dance may be providing honest cues to physical condition, and that females would have developed perceptual abilities to detect such cues. These authors investigated whether PT exposure (as measured by 2D:4D) was related to male dance quality as rated by females. The authors proposed this because previous research had often suggested that the organising effects of testosterone in utero plays a key role in sex differentiation, with high exposure leading to masculinised features, and it is thought to be a mediator in women's preferences for dominance, assertiveness and social status (Manning, 2002; Neave et al., 2003). To record men's dances, a standard video recording was taken which was later blurred to eliminate physical features as much as possible from the recordings, and standardised white overalls were provided to standardise clothing appearance. Female observers (N=104) rated a short 10s clip of each dancer (N=12) on attractiveness, dominance, and masculinity. Results indicated that women rated dancers with lower 2D:4D (high PT exposure) as more attractive, dominant and assertive, suggesting that dance is conveying higher-order information to females, which the authors speculated was related to aspects of mate choice.

This theory of dance being an honest cue of male condition has also been briefly extended to female dancers (Miller et al., 2007). Rather indirectly, the authors suggested that when female lap dancers were in their fertile ovulatory phase they earned more tips from clients. The authors also found that pill-users did not show this earnings peak. Miller and

colleagues speculated that during these dances, female movements 'leak' or 'signal' cues to their fertility and this is seen as 'sexier' to male observers.

More direct evidence for dance as an honest cue comes from Hugill et al. (2009). Following the findings of Fink et al. (2007) who found associations with testosterone, Hugill and colleagues attempted to link the testosterone related trait of physical strength to male dance quality. Physical strength is thought to be a highly valued trait in our evolutionary heritage and females should thus be seeking honest cues to it. To test this, the authors recorded 40 non-trained males dancing to a core rhythm track. In addition, two maximal force handgrip strength measures were conducted on each hand, and the mean of these measures used as a proxy for general strength. 50 females then rated the blurred dance videos. As expected, stronger males were rated as significantly better dancers, thus supporting the hypothesis that aspects of physical condition are encoded into male dance movements, and that females are sensitive to cues of such traits. This finding also supports the supposition that testosterone is a possible mediator between such dance movements and strength (Fink et al., 2007).

To conclude, brief inroads into the assessment of male mate quality from dance movements have been made in humans. Because of its close similarity in description to animal courtship displays, researchers have discovered that dance is indicative of traits that are desirable from an intersexual perspective. Researchers have found that several traits of reproductive quality are related to male dance performance, such as PT exposure, physical strength and fluctuating asymmetry. This research has attempted to control for static morphological traits by using blurred video clips and standardised clothing (Fink et al., 2007; Hugill et al., 2009), however these methods do not fully control for these features, and the blurring effect degrades stimuli making it sometimes difficult to see small movements. Other

research has employed a more robust method of controlling for such variables using 3D motion capture point-light based systems and applying ellipsoid figures to mask static features (Brown et al., 2005). Whilst this methodology is preferable over the blurred video clips, this still does not represent the ideal because the figure reduces the human motion down to a very basic skeletal frame (much like point light) that does not readily show rotations in the limbs or a full human-like shape.

1.8. Overall Summary and Project Rationale

Evolutionary theory informs us that mating with a healthy mate is paramount for survival and successful transfer of genes. In most species, the sex that chooses the mating partner is the female because of her higher parental investment. Females typically look for indicators of health and condition to ensure her partner has robust genes as well as the potential to protect and acquire resources (for example the ability to hunt). The problem with many of these facets is that they can sometimes be hard to observe because of clothing or low light or not observable directly at all (e.g. health) and must be inferred from cues or signals. Females should look for honest indicators of such traits that cannot be faked by the host. These cues or signals take many forms and vary from species to species. Many mammals lack conspicuous ornamentation such as bright plumage that appears to provide cues to physical condition and immunocompetence. As a result, other means of assessment must be made. Very subtle static cues have been the focus of the majority of research (using 2-D methodology); such cues often have quite robust effects especially in areas such as FA and facial attractiveness. However, as these features are often very subtle, doubt has been cast as to whether these traits can be discriminated in the real word. This point has led researchers to examine a very observable facet of life: movement. Many researchers believe movement is a more useful cue to condition as it relies so heavily on many of the body's systems that it is impossible to fake

good quality movements. This paired with the observation that many animal species perform ritualistic, vigorous and skilful courtship displays supports such a supposition, and researchers have attempted to link these displays to reproductive quality. Transferring this aspect of research in animals to humans has been made somewhat more difficult because isolating movement cues from other important features of mate choice such as facial attractiveness, height, and build is difficult. Point-light methodology derived from the field of biological perception has proved invaluable as it excludes most of these variables. It has been noted that the human visual system is extremely adept at deriving higher-order characteristics from brief presentations, these include intention, sex, emotion and action. This methodology has since been applied to questions pertaining to movement's role in sexual selection in humans with some success. These studies have used dancing because it is a form of intentional, exaggerated rhythmic movements that best fits what many animal anthropologists term a courtship display. Such research has found that dance quality has positive links with developmental stability, strength and PT exposure, traits known to be of importance in female mate choice decisions. However, such studies have often used impoverished blurred stimuli or extremely basic ellipsoid figures in an attempt to mask static cues.

The aim of the current thesis is to establish a new methodology based on accurate 3D motion capture hardware that has recently become available (similar to the equipment of Brown et al., 2005 and Troje, 2003) paired with professional animation software to fully eliminate static cues that could interfere with perceptions whilst maintaining a realistic, human form not reliant on degrading stimuli.

Using this methodology, the main focus of this thesis will be to further examine established pertinent physical and psychological traits of interest in mate choice and discern whether these can be detected via male dance movements. Furthermore, the research programme aims to add an additional layer of depth to such research by considering if

specific movement characteristics in particular are influencing female perceptions through biomechanical analysis.

The research programme therefore aims to test the following research questions:

1. By using a new methodology using both 3D motion capture hardware paired with professional animation software, can the same level of perceptual accuracy in sex discrimination be observed that is reported in previous point light research (methodological validation)?
2. Which movements predict good and bad male dancers as rated by female observers?
3. Is health-related information encoded into male dance movements, and is this reflected in observer's assessments of dance quality?
4. Are cardiovascular fitness and strength encoded into male dance movements and are these reflected in observer's assessments of dance quality? It is predicted based on previous research on faces (Sell et al., 2009) and dancing (Hugill et al., 2009) that strength will be reflected in observer judgements. However, the extent to which cardiovascular fitness is observable is disputed in static cue research (Honekopp et al., 2004; Williams et al., (2010).
5. Is age encoded into male dance movements and is this reflected in observer's assessments of dance quality?

CHAPTER 2: GENERAL METHODS & METHODOLOGICAL VALIDATION

2.1. Background

A variety of methodologies have been used to control for the majority of static cues that may confound mate choice based research. However many of these so-called point-light methods do not control for height and build at an individual level. The other disadvantage of this, especially when considering complex movements involving rotational movements like dancing, is that point-light displays can sometimes be unclear with regard to the way the actor is facing because of the symmetry of the marker layout. However, basic point-light methods are currently the gold standard baseline for recording movement with accuracy (Troje, 2003; Sigal & Black, 2010) as other methods such as quantising (Berry, 1991), or blurring (Fink et al., 2007; Hugill, 2009) of standard video displays rely on degrading stimuli to produce such sparse cues. Furthermore, current optical based motion capture systems allow for the extraction of biomechanical information allowing users to quantify movement for use in objective analyses. A more realistic figure can then be attached over the top of the point-light information (as in Brown et al., 2005). Initially this poses the question of whether the additional form information presented alters perceptions. McDonnell et al. (2008) however addressed this issue in their study investigating motion perception from point-light vs. avatar (virtual character) stimuli. It was found that motion and not body representation dominated the perception of portrayed emotion, suggesting that avatars do not significantly influence participants' perceptions over the biological movement itself.

Other considerations for methodology include which viewpoint to display stimuli in. Early research used side-view point-light animations of walkers for the assessment of sex

(e.g. Cutting & Kozlowski, 1977) however more recent research suggests the most pertinent motion cues are available from frontal view (Troje, 2003). Furthermore, many point-light studies do not include markers on the hand but only the arms. Atkinson et al. (2004) suggested that hand markers are a key characteristic for displaying emotional intent and so should be included in studies attempting to look at high-order social information cues. With these considerations in mind, a highly accurate, point-light 3D optical motion capture system will be utilised alongside professional animation software to add an additional layer of realism without sacrificing control of static variables to record and display male dance movements to female judges.

2.2. General Method and Setup

Vicon motion capture systems (Vicon, Oxford Metrics) rely on placing small optical markers on a participant's body in a set pattern in order to capture all the main joint and body kinematics. Several specialised high-speed cameras surround the capture space and emit near-infrared beams that 'bounce' off the reflective markers on a participant's body, thus giving the camera precise coordinates of all the markers in 3D space. It is also possible to extract precise movement kinematic coordinates and angles for additional gait analysis. Systems such as this are often used for clinical gait analysis following joint replacements. The following motion-capture equipment setup was utilised for all studies in this thesis.

2.2.1 Hardware

A 12-camera Vicon MX system was used which consisted of;

Core processing unit

Two MX-giganet core control units were used for optimum efficiency. Both units incorporated gigabit Ethernet for camera and PC data connections. This allowed for 1000mbps data transfer allowing for a real-time reconstruction of the motion-capture space at a smooth frame rate.

Cameras

Twelve Vicon MX T-20 cameras were used to record movement. Each T-20 camera emits a near-infrared strobe beam in order to accurately capture reflective markers. The T-20 cameras utilise custom CMOS (Complementary Metal–Oxide–Semiconductor) digital image sensors rather than CCD (charge-coupled device) in order to give both high resolution as well as high speed with the principle benefit of being completely digital. Each camera was setup at a resolution of 1600x1280 using a capture frame rate of 200 frames per second (200Hz) to aid in the capture of particularly vigorous movements. Camera positions and lab layout are shown in figure 1 (See appendix A).

2.2.2 Participants (dancers)

Each male participant was recruited using opportunity sampling for the study, and were screened to eliminate professional dancers, and men who had any physical injuries that could have affected their movements.

2.2.3 Participant Measurement

Vicon Nexus software is predominantly used for biomechanical analysis (the studies reported in this thesis used versions 1.05-1.7). In order to extract accurate kinematics of joint angles and trajectories, various measurements must be taken from each participant and entered into the Nexus software. Such measurements are also used to create a labelling model that allows for the automatic labelling of markers. The following measurements must be taken:

Height (mm) (stadiometer, SECA)

Weight (kg) (scales, SECA)

Leg length (mm) (measuring tape)

Ankle width (mm) (digital vernier calpiers)

Knee width (mm) (anthropometer)

Elbow width (mm) (digital vernier calpiers)

Wrist width (mm) (digital vernier calpiers)

2.2.4 Marker-set

Markers were attached to participants in accordance with the Vicon Plug-In-Gait marker set (see figure 2). The marker setup consisted of thirty-nine 14mm round reflective markers placed at the major joint locations on the body. The Plug-In-Gait full body marker layout is arranged so that there are several markers on the same rigid structures of the body (for example there are four markers on the head and five on the torso). This allows for easier data fixing when markers become occluded. The Plug-In Gait marker set has been validated by several biomechanics researchers (for example: Davis, et al., 1991; Kadaba et al., 2005) and provides accurate representation and output of joint kinematics.

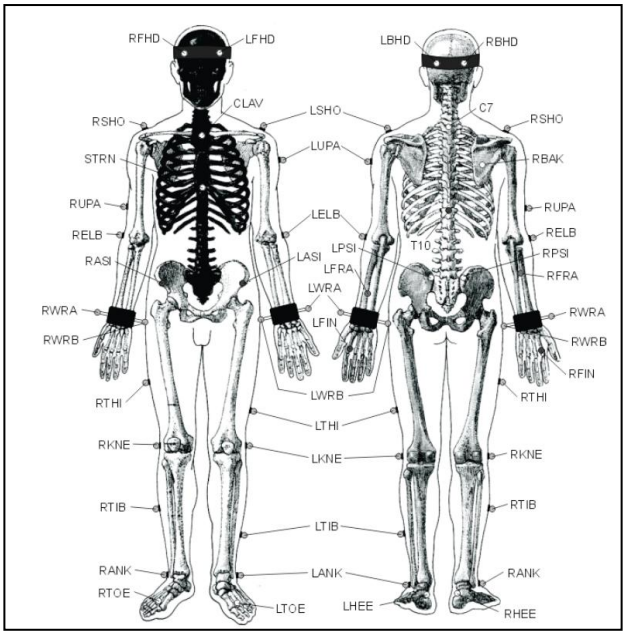

Figure 2*. Plug-In Gait marker set layout showing the anatomical locations of each marker on the body (Vicon, Oxford).*

In order to ensure accurate placement of markers on the body, participants were asked to wear shorts, be bare-footed and either wear a tight fitting t-shirt or be topless. This greatly enhanced the accuracy of the movement recorded (see figure 3).

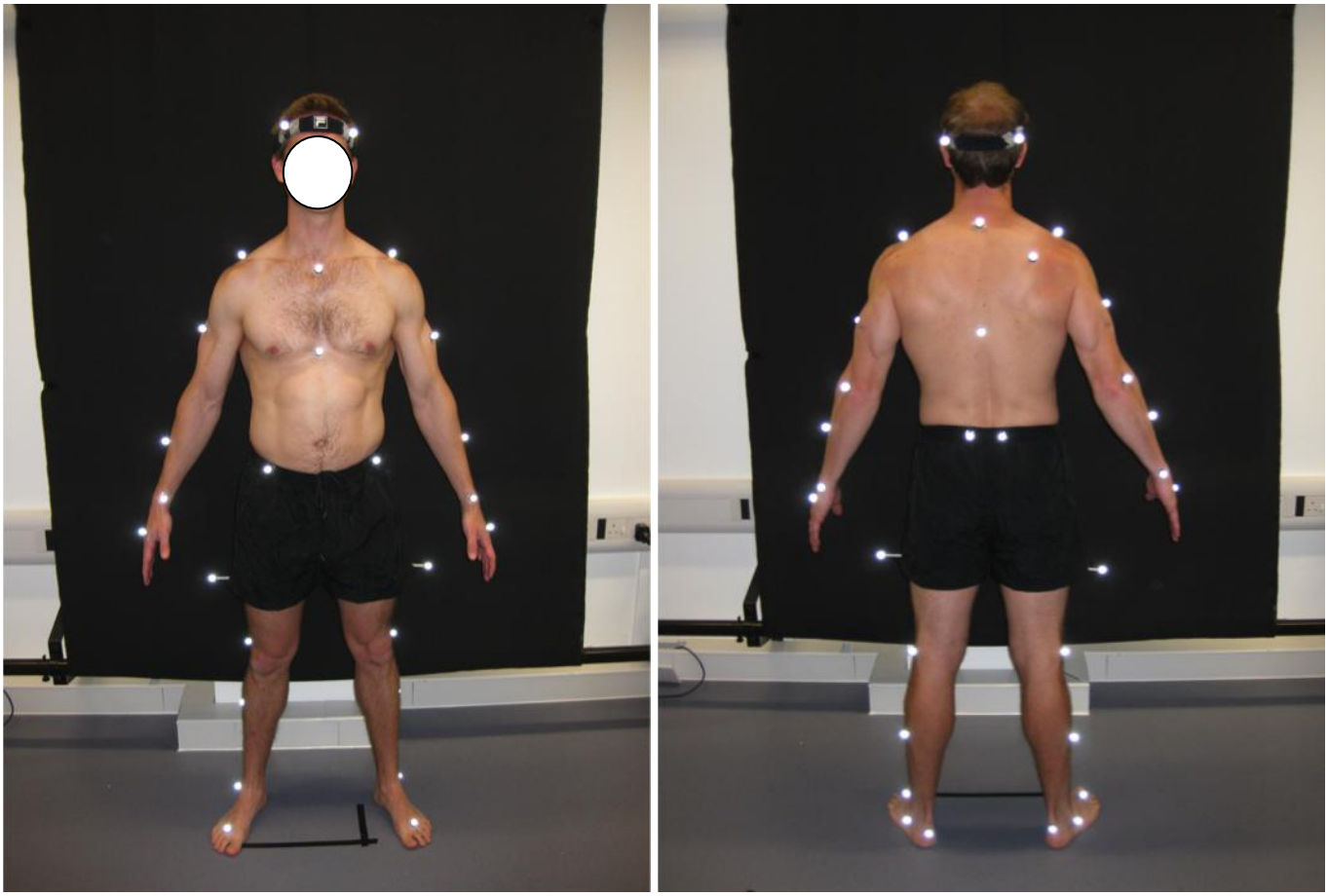

Figure 3: *Participant labelled using the Plug-In-Gait marker layout.*

2.2.5 Data Capture

Markers were placed at the anatomical locations as indicated by the Plug-In-Gait marker set (see Figures 2, 3) and participants asked to stand at the point of origin in the lab (centre of the lab) in a T-pose; a static position in which the participant stands with their feet shoulder width apart, arms raised to shoulder height, palms facing down. A 600-frame snapshot was then taken. This calibration snapshot was then labelled to check for any missing markers. If any anomalies in the data were found or if any markers were missing, this T-pose recording

was repeated. Following the T-pose, participants were asked to dance for 30 seconds to a core 125bpm drum beat (so that music likability could not affect expressiveness of dance movements). Approximately 6000 frames are captured for a 30 second trial (at 200Hz capture rate).

2.2.6 Data Processing/Cleaning

Once the dance trial was recorded, it was then labelled throughout. Nexus software can create an automatic labelling model based on the participants T-Pose and measurements in order to speed up the labelling process. However it does not fill any gaps in the data (where a marker disappears and reappears), these typically occur when another body part occludes a given marker.

Occlusion: One of the biggest issues when using optical motion capture systems is occlusion. In order to eliminate noise in optical data (i.e. cameras picking up reflections in the environment, also known as ghost markers) Vicon Nexus software only recognises and reconstructs markers if three cameras detect a given reflection, and it is seen as round in shape. Occasionally this causes problems with real markers placed on participants. If a participant moves in a certain way in which to hide or 'occlude' a marker, fewer cameras see the marker (for example a hip marker being occluded by the participant's arm). The space in-between a marker first disappearing and reappearing is called a 'gap'. Such gaps can often be filled using the Nexus software, which uses the pattern of movement from other markers on the same segment of the body (for example filling an anterior hip marker with the posterior one from the same side). For the purposes of accuracy, filling gaps in excess of 30 frames (at 200Hz capture rate) is not recommended in Vicon Nexus as this makes the extraction of precise kinematic angles inaccurate. In instances where a gap is more than 30 frames in length, it is recommended that the running of biomechanical extraction models (such as Plug-

In-Gait) be executed with the gap present. This is because the software's algorithm for copying the pattern of other markers to fill the gap is not precise enough for large gaps, and the model manual advises against this.

Crossover: Crossovers can occur in optical data when two markers come very close to one another. The Vicon Nexus software confuses the two markers and swaps their positions. When this occurs, the data (both kinematic and optical) becomes unusable. Therefore, it is essential that all crossovers are dealt with. There are two possible remedies to this; one is to create gaps in the markers where a crossover is present (i.e. delete the markers for the duration of the crossover) and using the gap filling command. The other is to try and manually swap the markers although this typically creates problems with other parts of the trial.

Biomechanical Extraction: Vicon motion capture systems allow for the extraction of precise 3D (*x*,*y*,*z*) angle biomechanics. The Plug-In-Gait kinematic model (Vicon, Oxford) was used in the extraction of three-dimensional joint angles for the knees, hips, trunk, neck, shoulders and wrists. Ankle angle was only calculated in two dimensions (flexion/extension and internal/external rotation) and the elbow in one dimension (flexion/extension). Before the extraction process a low-pass Butterworth filter (10Hz) was applied to each joint angle to 'smooth out' the angles trace before extraction, as the raw data tends to be unnecessarily noisy due to the high accuracy of the system.

Vicon Nexus extracts 74 separate angle variables based on the Plug-In-Gait model for every frame in the trial thus creating an extremely large dataset. Not all of these angles are meaningful to the type of study. For example, Nexus extracts both left and right spine angles that have identical properties. This also occurs in the neck angles. In these cases only the left properties of these structures were used. Other information such as foot progress coordinates

(used in the analysis of foot placement in walking and running, e.g. forefoot first, heel strike first) are only used in walking analysis and were thus dropped. The remaining 32 angles were summed together into their relative body segments to make them easier and more meaningful to interpret. Figure 4 summarises the grouping process.

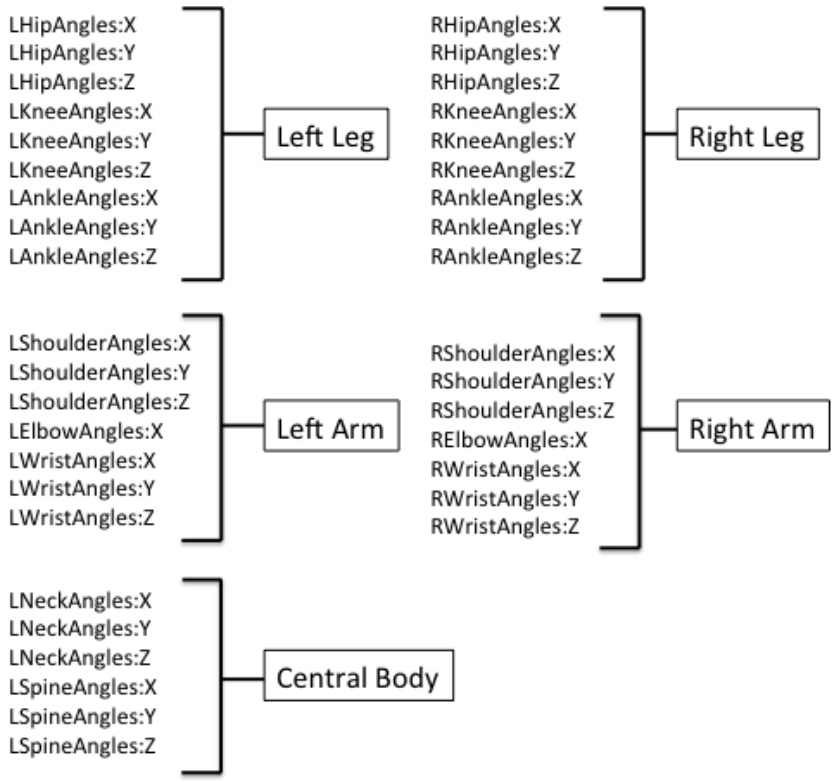

Figure 4: *Breakdown of biomechanical variables into relative body segments*

There is virtually a limitless variation in the type of motion data that can be extracted, however because of the novel and exploratory nature of this research, basic measures of movement *speed, amplitude, variability* and *duration* were taken. These variables are not without theoretical underpinnings; Byers, et al. (2010) indicate that in the animal kingdom vigour (i.e. *speed/duration/amplitude*) is of particular importance. *Variability* may on the other hand be a basic measure of movement ability as repetitive, non-variable movements for example may reflect mental or physical deterioration or disability.

Movement variables of interest were calculated in Mathworks MATLAB (v.2011a). *Duration* was defined as the time between successive reversals in direction. For example time taken to extend the forearm from the elbow and then return to its starting position. *Amplitude* was the magnitude of change from the mean joint position of the entire trial for example a large movement of the arm would be a full extension from the elbow. *Speed* of each angular movement was calculated as the amplitude divided by the duration for example a fast arm extension. *Variability* was calculated as standard deviation of all angular offsets for each joint for example, a continuous small head nod movement would not vary greatly from the mean head position whereas a small head nod followed by a larger head nod would represent greater deviation from the mean head position.

2.2.7 Post-Processing Software (AutoDesk MotionBuilder 2011)

Due to the nature of Vicon, the Nexus software does not control for height and body shape as it accurately maps the participant's body shape and size using the optical markers. This creates two fundamental confounds which could directly influence female judgments of male movements (Lippa, 1983). In addition, Nexus software does not provide a realistic representation of a human (only a wireframe is reproduced). In order to address these confounds, the optical data from Vicon was exported into the professional animation software Autodesk Motionbuilder (Autodesk inc. v2009-2012). Using the optical data as a control mechanism for standardised avatar (virtual person) eliminated the confounding variables of height and body shape while giving the motion a more human-like shape. The avatar chosen for presentation was a featureless humanoid coloured grey/white (see figure 5).

Gaps in the Vicon data must not exceed 30 frames for the gait model to be accurate. In Motionbuilder, these large gaps degrade the resulting animation; therefore any remaining gaps from Vicon must be fixed. Motionbuilder has functions in place that allow it to

accurately fill larger gaps by creating a virtual 'rigid body' marker which essentially maintains the shape and pattern of a selection of markers. If a marker disappears and reappears, the resulting model is not affected by the gap. Such virtual markers are represented in red as opposed to the blue colour of regular optical markers. In order to accurately animate an avatar, it is first necessary to recreate the exact characteristics and stance of the participant by shaping a deformable 'actor' to fit the optical markers. Essentially this means lining up each marker with its exact location on the participant's body (See figure 6).

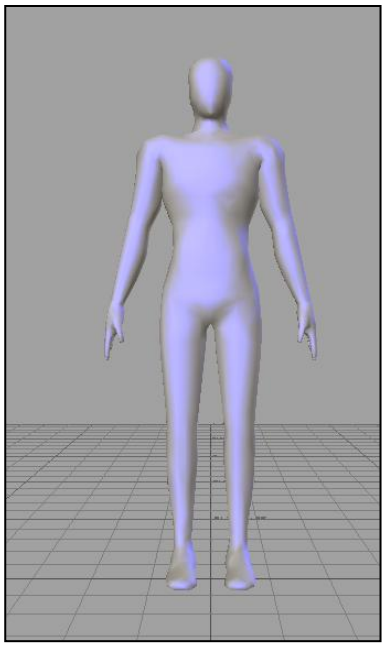

Figure 5. Avatar model used in Motionbuilder

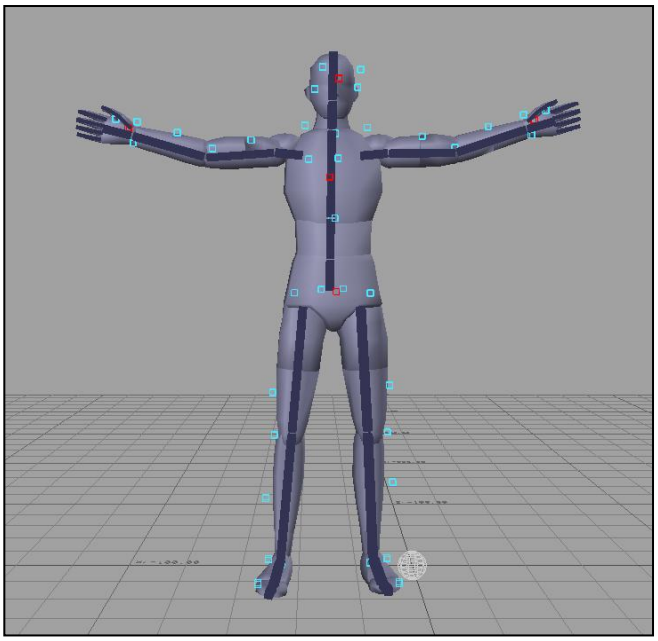

Figure 6. Motionbuilder actor model fitted with optical data

By default Motionbuilder does not recognise the layout of the Plug-In-Gait marker set. Therefore it must be defined in the actor settings (See figure 7), which specifies which markers drive which segments of the body. Table 1 (Appendix A) summarises which markers were chosen to drive which parts of the actor.

Once the actor has been rigged with the marker set, it is then animated and checked to ensure smooth motion throughout. It is then hidden from view and an avatar is inserted into the scene.

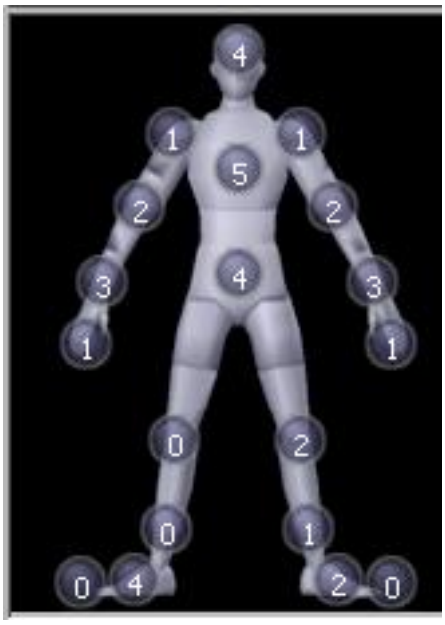

Figure 7: Actor model's distribution of optical markers. NB; the numbers on the figure represent how many optical markers are driving that segment of the body, for example, four head markers are driving the head portion of the body.

Motionbuilder files (.fbx) cannot be played back using standard video playback software (e.g Windows Media Player). So in order to facilitate this, the resulting dance animation was then recorded in a 1024x768 window from a laptop screen with a resolution of 1900x1200 using freeware screen recording software CamStudio (http://camstudio.org/). For purposes of manageable file size, each .AVI file was encoded and compressed using Xvid. This had no noticeable impact on the quality of the file. Each 30-second dance was trimmed in length down to 15 seconds using SolveigMM AVI Trimmer (http://www.solveigmm.com/). It was decided that the middle 15 seconds of a dance would be presented to judges as it allowed for dancers to become accustomed to their environment

and adapt to the rhythm of the music. This was applied throughout all the studies reported in this thesis.

2.3. Rating Studies

2.3.1 Participants

Participants were sourced using opportunity sampling and varied study to study based on compensation for their time.

2.3.2 Presentation of rating studies

In all studies presented in this thesis, each of the avatar videos was rated on several attributes. While the specific rating attributes differed slightly between studies, a common way of presenting the videos was employed in each case. Empirisoft MediaLab 2008 (Empirisoft Inc. New York, USA) was used to present the dancing avatars to rating participants. MediaLab is a flexible program developed for use in psychology research. It allows for complete control over presentation of various kinds of media files, and participant input is written to comma delimited .csv files. MediaLab was configured to show black backgrounds with white text throughout at a resolution of 1900x1200.

After an initial welcome screen, instructions for participants were presented, followed by a priming slide simply informing them to "click continue to see the dancer". The 15-second clip was then played in the middle of the screen. After presentation of the dance clip, participants were asked to rate the dancer they had just seen on several attributes on a 7-point

Likert-type scale (1= low scoring on a given attribute, 7= high scoring on a given attribute) that differed study to study. Clip order was randomised for each participant.

2.4. Ethical Statement

Ethical approval was granted for all studies reported by Northumbria University School of Life Sciences Ethics Committee, acting in accordance with Northumbria University Research Ethics and Governance Handbook. The following code numbers apply (study 1 = SUB50_KM; study 2-3 = SUB08_NN; study 4-5 = SUB005_KM)

2.5. Study 1: Validation Study

In order to validate the above methodology, a simple sex recognition task was utilised.

2.5.1. Method

Participants:

Stimuli Participants: An initial sample of ten participants (five male) was recruited from the Northumbria University post-graduate population aged 18-25 years (M = 24.7, SD = 15.7), none of whom had any injuries that could have affected their movement. One female participant was dropped from the study as gaps in the optical data prevented accurate avatar creation thus, nine participant walks (five male, four female) were presented to judges.

Rating Participants: Five male and five female participants were recruited from the Northumbria University post-graduate population.

Motion Capture/Avatar creation: Following the above equipment setup and upon completing a T-Pose calibration, participants were asked to walk up and down a ten-metre walkway at normal walking pace until asked to stop. The investigator looked away from the participant and did not reveal that their walk was being recorded in order to reduce conscious awareness that may have produced artificial movement. After a suitable-length walking trail was completed (usually after the participant had walked in both directions three times), participants were fully debriefed and made aware of the nature of the study. Avatars were created using one complete 10m walk which was usually around five full gait cycles taking approximately five to six seconds to complete. This was then recorded on a continuous loop for 15 seconds from frontal view (as this view grants the most information to the viewer, Troje 2003) to allow participants ample time to make a judgement. Recordings were taken from the middle-end of a session to allow for participants to relax into the task. All recordings were captured at a 1024x768 resolution.

Rating study: Rating participants viewed each of the nine walking avatars. Clip order was randomised for each participant and each rater provided a forced-choice judgement of the walkers' sex.

2.5.2. Results and Conclusion

On average, participants accurately judged the sex of a walking avatar 82% of the time. Table 2 shows percentage correct judgments of sex per avatar. Note that male 3 was incorrectly identified as female 60% of the time suggesting either a problem with the animation or a naturally more feminine walk. Raters themselves were more accurate than chance, Table 3 shows individual rater performance on the task.

Table 2. Percentage correct gender identifications of male and female judges (N=10)

Avatar	% Correct
Male 1	100%
Male 2	60%
Male 3	40%
Male 4	100%
Male 5	100%
Female 1	90%
Female 2	80%
Female 3	100%
Female 4	60%

Table 3. Rater performance (% correct of 9 avatars) on the sex identification task

Rater	Correct classification
1	100%
2	77.78%
3	100%
4	66.67%
5	88.89%
6	100%
7	88.89%
8	66.67%
9	66.67%
10	77.78%

Cutting and Proffitt (1981) suggested that one key difference in the gait of men and women is that men walk faster (i.e. stronger stride) than women. The walking avatars presented in this study did not control for such differences. However, based on the quite short gait cycles (that were merely looped) presented this was probably not visible. Furthermore Cutting and Proffitt (1981) stated that even when speed is controlled, sex identification was just as accurate.

In conclusion, participants correctly identified the sex of the walking avatar more than 80% of the time, a level comparable to that reported by Troje (2003) using point-light stimuli.

This indicates the chosen methodology is a valid way of recording movement without previous confounds such as body size/weight/attractiveness etc whilst still providing accurate human movement kinematics.

CHAPTER 3: STUDY 2, WHAT MAKES A GOOD MALE DANCER?

3.1. Background

In chapter 2, the methodology to be used in this thesis was successfully validated against the previous point-light technique as described by Troje (2003). In a simple sex recognition task the use of more realistic avatars was comparable to that of point-light animations, with the avatars not impacting on the robust recognition of higher order information.

The aim of this thesis is to explore the hypothesis that male movements are providing honest cues to qualities that are important to female observers. To address these aims male dance moves have been chosen because they comprise a set of intensive, dynamic rhythmic movements that might be expected to clearly advertise male physical and behavioural qualities. Previous studies have indeed indicated that cues to physical condition, PT exposure and physical strength appear to be encoded into such dances (for example; Fink et al., 2006; Hugill et al., 2009).

A key question that relates to the signalling properties of male dancing is what actually makes a 'good' dancer? Whilst previous studies (Fink et al., 2003, 2006; Hugill, 2009) have found links between female ratings of dance quality and men's physical strength (thereby providing some evidence in support of the 'honest cue' hypothesis), they have not speculated upon which specific aspects of dance movements are conveying such information.

The aim of this study was therefore to record a sample of male dancers, convert their motion-capture data into avatars, obtain female ratings of their dance quality, and then extract precise biomechanical information from each dancer. The biomechanical information selected was mostly basic due to the preliminary nature of this thesis but somewhat derived

from comparative literature (e.g. vigour, Byers et al. 2010). These are explained in detail in Chapter 1.

3.2. Method

3.2.1 Motion capture and avatar creation

The methodology used to record male dance moves, extract biomechanical information, and convert the motion-capture stimuli into avatars has been fully explained in chapter 2.

3.2.2 Participants

Male dancers: An initial sample of 30 male participants were collected as dancing stimuli (mean age=22.72, sd=4.37) in the investigation.

Female Raters: 37 heterosexual women aged 18-35 (mean=22.30, sd=6.22) rated each of the male dance avatars on dance quality using a 7-point Likert-type scale (1= extremely bad dancer, 7= extremely good dancer). Ratings were presented as outlined in section 2.3. Cronbach's alpha determined high inter-rater reliability (α=0.94) so subsequent analyses were based on mean ratings for each male dancer.

3.2.3 Biomechanical analysis

The extraction process described in section 2.2.5 led to 11 out of the 30 male dancers to be excluded from further analysis because of incomplete or faulty biomechanical output, leaving 19 male dances for complete analysis.

3.3. Results

Normal distribution of each region and movement variable were checked using Kolmogorov–Smirnov tests. All but two movement variables were normally distributed (variability of the neck flexion/extension and trunk internal/external rotation was not); in these cases Spearman's rank correlations were conducted. Initially, Pearson product–moment correlations were performed between mean ratings of dance quality and each of the three body regions for movement amplitude, movement variability, movement speed and movement duration. If a significant correlation was found for any one body region, a further correlation was performed between ratings of dance quality and the constituent parts of that body region. An alpha level of .05 was used throughout. A summary of the correlations is presented in table 4.

For movement amplitude, all body regions were normally distributed. Significant positive correlations were found between dance ratings and the central body region. Key components comprised of: neck flexion/extension (head nodding), trunk flexion/extension (forward/backward bending), and trunk abduction/adduction (sideways bending). For movement variability, all three body regions were normally distributed, although seven of their 38 constituent parts were not. Significant positive correlations were found between dance ratings and central body region variability with all components being important, these were: neck flexion/extension; neck abduction/adduction (head sideways tilting); neck internal/external rotation (head shaking); trunk flexion/extension; trunk adduction/abduction; and trunk internal/external rotation (twisting). Finally, for movement speed, all data were normally distributed. Significant positive relationships were found between speed of the legs and dance ratings, the relevant components being speed of right knee flexion/extension (bending) and speed of right knee internal/external rotation (twisting).

When the significant constituent parts were fed into a stepwise linear regression to predict dance ratings, neck internal/external rotation variability (β =0.29), trunk

adduction/abduction variability (β=0.46) and right knee internal/external rotation speed (β= 0.38) contributed to the final model ($F_{3,15}$ = 18.9, p =<0.001), which accounted for 79% of the variance in the mean dance ratings.

Table 4: Correlations between movement variables and ratings of dance quality. Correlations or sub-components are only presented when the principal component was significantly correlated with dance rating.

	Movement Amplitude	**Movement Variability**	**Movement Speed**
Arms	r =0.45; p =0.051	r =0.44; p =0.057	r =0.34; p =0.153
Central Body	*r =0.55; p<0.05	*r =0.81; p<0.001	r =0.41; p =0.082
Neck Flexion/Extension	*r =0.47; p<0.05	*†r =0.68; p<0.01	n/a
Neck Abduction/Adduction	r =0.30; p =0.219	*r =0.66; p<0.05	n/a
Neck Internal/External Rotation	r =0.38; p =0.113	*r =0.73; p<0.001	n/a
Trunk Flexion/Extension	*r =0.67; p<0.01	*r =0.68; p<0.01	n/a
Trunk Abduction/Adduction	*r =0.48; p<0.05	*r =0.68; p<0.01	n/a
Trunk Internal/External Rotation	r =0.08; p =0.734	*†r =0.51; p<0.05	n/a
Legs	r =0.24; p =0.332	r =0.23; p =0.334	*r =0.47; p<0.05
Right Hip Flexion/Extension	n/a	n/a	r =0.21; p =0.393
Right Hip abduction/adduction	n/a	n/a	r =0.02; p =0.925
Right Hip Internal/External Rotation	n/a	n/a	r =0.23; p =0.337
Right Knee Flexion/Extension	n/a	n/a	*r =0.52; p<0.05
Right Knee abduction/adduction	n/a	n/a	r =0.24; p =0.317
Right Knee Internal/External Rotation	n/a	n/a	*r =0.70; p<0.01
Right Ankle Flexion/Extension	n/a	n/a	r =0.40; p =0.100
Right Ankle Internal/External Rotation	n/a	n/a	r =0.24; p =0.329
Left Hip Flexion/Extension	n/a	n/a	r =-0.01; p =0.963
Left Hip abduction/adduction	n/a	n/a	r =0.02; p =0.944
Left Hip Internal/External Rotation	n/a	n/a	r =0.31; p =0.200
Left Knee Flexion/Extension	n/a	n/a	r =0.31; p =0.193
Left Knee abduction/adduction	n/a	n/a	r =-0.03; p =0.901
Left Knee Internal/External Rotation	n/a	n/a	r =0.34; p =0.160
Left Ankle Flexion/Extension	n/a	n/a	r =-0.04; p =0.886
Left Ankle Internal/External Rotation	n/a	n/a	r =-0.11; p =0.646

3.4. Discussion

The results indicate that there is a general consensus among women about male dance quality and the extraction of biomechanical characteristics that describe dance are on the whole successful. Key predictors of dance quality ratings were amplitude and variability of the upper body (trunk and neck) as well as speed of the right knee. Put in the context of real 'moves' in a nightclub for example, those dancers judged as being better, had larger, more varied movements of their upper body (head, neck, and trunk) which translates to swaying and twisting of the chest and shoulders as well as moving their right leg (specifically bending of the knee) faster, perhaps whilst standing on their left foot for support. Whilst initially the speed of just the right knee seems rather unintuitive, the majority of the population are right-footed (Coren, 1992) so this is perhaps not surprising as participants may be standing on their non-dominant leg (left) and flexing and extending their dominant leg (right) as this feels more comfortable. In contrast, those rated as bad dancers have smaller and more monotonous movements. This might include simple head nodding with very little movement in the trunk.

As this was the first investigation into the biomechanical variables associated with dance using this methodology, a large percentage of the initial sample (11 out of an initial 30) male dances could not be used in the analysis due to incomplete or troublesome data. This left a relatively small sample and so replication with larger samples would be desirable. In subsequent studies, these issues will be addressed at the data acquisition stage to avoid unnecessary data loss due to missing markers and incomplete models. Thus, larger data sets (30+) of complete male data with greater variability will be collected and subjected to the same biomechanical analysis in order to form stronger conclusions.

This study did not however investigate whether these movements are indicative of actual condition or whether physical condition underpins female preference. The remaining

chapters of this thesis will thus explore these biomechanical characteristics and attempt to link them to desired traits in males such as health (Buss & Schmidt, 1993) physical fitness and strength (Hönekopp et al., 2006; Manning, et al, 2007; Hugill et al., 2009), and age (Buss, 2004) as presumably these traits significantly influence motor control.

CHAPTER 4: STUDY 3, MALE MOVEMENTS AS POSSIBLE CUES TO HEALTH AND SYMMETRY

4.1. Background

In chapter 3, it was discovered that females displayed a consensus as to what constituted a 'good' and 'bad' male dancer. Movements that were greater in variability and size, particularly of the upper body were key factors in female perceptions of male dance quality. Of key importance in all intersexual mate choice decisions are that females mate with high quality males. Theoretically this is important for a two key reasons; firstly that mating with an unhealthy male leads to the deleterious effects of his gene pool being passed on to any offspring and secondly, the male has a heightened risk of death from disease, and therefore could be unable to provide resources for the female and her offspring. Byers et al., (2010) suggests that movements that display vigour and skill should provide honest cues to the health status of an individual.

In humans, dancing has long been a ritual that mimics the definition of a courtship display and more recently researchers have begun investigating whether it hold cues to condition in males. Brown et al. (2005) for example found that better rated dancers were more symmetrical and Fink et al. (2006) found that dance quality in men was associated with higher PT exposure *in utero*. To the author's knowledge no studies yet have explored possible relationships between male physical performance (dance) and their health.

The current study thus aims to explore whether male dance conveys information to females about his physical condition, current physical and mental health status and explore whether these facets are linked to the biomechanical variables outlined in chapter 3.

4.2. Method

4.2.1 Motion Capture & Stimuli Creation

The Vicon motion capture system was set up as outlined in chapter 2.

4.2.2 Participants

78 males aged 18-42 (age M= 21.63 years, SD= 4.06) participated in the study. Participants were paid £10 to compensate their time.

4.2.3 Symmetry and physical measures

Participants' % body fat (Tanita TBF-521 body fat scale), resting heart rate and blood pressure (Omron M3) were measured in addition to the normal biomechanical measurements taken (see section 2.2.3). The following 13 body symmetry measurements were taken from each participant (closely mirroring the measures used by Brown et al., 2005);

- 2^{nd}, 3^{rd}, 4^{th} and 5^{th} finger digits (mm) using Mitutoyo Absolute digital vernier digital callipers.
- Hand, wrist, elbow, knee, ankle and foot widths (mm) measured using a Lafayette model 01291 anthropometer.
- Leg lengths (cm) measured using Seca measuring tape.

All traits were measured in turn and then the procedure was repeated. The mean of the two measurements was used in the analysis to help reduce measurement error. Symmetry was calculated in accordance with Palmer (2004) whereby a sample of more than 10 body traits were measured and adjusted for trait size in order to eliminate particularly large traits having seemingly greater variability than small ones. The following equation was used:

ABS(R-L) / 0.5 * (R+L)

Here, absolute symmetry (ABS, R-L) is divided by the average of the trait size thus eliminating (standardising) large traits showing greater deviations from the mean than small traits. Cronbachs alpha was computed on the corrected traits as a measure of reliability and reported a low statistic (.23) meaning caution must be taken in any significant relationships and interpretation.

4.2.4 Subjective physical and mental measures

Several self report physical and mental health questionnaires were chosen to assess the current and recent health status of each participant:

- **Minor Health Complaints Checklist (MHCC) [Appendix B].** The MHCC is an in-house physical health questionnaire based on four subscales (indicators, immune challenge, atopic, gastric and fungal) in addition to a total ill health score. The measure is designed to assess a range of acute, recent heath complaints in the last month. Scoring consists of five sub-scales that combine (sum) three-five questions pertaining to immune challenge, atopic illness, gastric illness, fungal illness. In addition to these subscales, a total ill health score is also calculated based on the sum of all questions. The questionnaire is currently unpublished.

- **Profile of Mood States (POMS) (65-item standard).** The POMS was designed to assess fluctuations in mood among adults (McNair et al., 1971). The original 65 items questionnaire was used in the current study. The questionnaire measures the following six mood scales on a continuum: Tension-Anxiety, Vigour-Activity, Depression-Dejection, Fatigue-Inertia, Anger-Hostility, and Confusion-Bewilderment. Since its inception, the scale has been validated and successfully applied in several populations

(in both adolescents and adults) and cultures (Terrya et al., 2003; Beediea et al., 2000; Yokoyama et al., 1990) as an accurate measure of mood states.

- **General Health Questionnaire (GHQ).** The GHQ was designed as a 12 item (in addition, 60, 30 and 20 item variants exist), Likert-type questionnaire designed to assess minor psychiatric disorders in community and clinical settings (Goldberg, 1972). Goldberg et al. (1997) reported that the short, 12 item scale was a particularly robust and reliable measure of minor psychiatric illness.

- **Beck Depression Inventory (BDI-II) (Beck et al., 1996a).** The BDI was first published in 1961 as a self-report questionnaire measure of depression, comprising of 21 sets of self-contained statements cored 0-3 (Beck et al., 1961). Since then, several revisions were made according to differing criteria laid out in the Diagnostic Statistical Manuals (DSM), the latest revision being the BDI-II (Beck et al., 1996a). Studies of the multiple versions of the questionnaire yield solid reliability coefficients and good convergent validity among one another as well as with other measures (this holds for both older and younger populations, in clinical and non-clinical groups) (Beck & Steer, 1984; Beck et al., 1988; Beck et al., 1996b; Segal et al., 2008).

4.2.5 Biomechanical analyses

In an attempt to ascertain possible mediators between dance perception and dancers' objective health, full-body biomechanical information was extracted from each dancer (Plug-In-Gait kinematic model, Vicon, Oxford). Joint angles were grouped into five main body regions and as outlined in chapter 3. Again, *amplitude*, *duration*, *speed* and *variability* were extracted for each, resulting in 20 biomechanical variables. It appeared that *duration* and *speed* variables were significantly negatively correlated (r = -.*37* between all summed duration variables and all summed speed variables) which may cause confusion in any

interpretation. To reduce ambiguity in further analysis, duration variables were dropped in favour of speed variables as literature from the animal kingdom suggests that speed (often termed vigour) is a key aspect of courtship displays (Byers 1994; Byers et al., 2010). The remaining 15 biomechanical variables were reduced further by conducting factor analysis (PCA, Varimax). A factor solution that closely follows the significant biomechanical characteristics and body regions outlined in chapter 3 emerged; Three factors which comprised of the following were extracted: *legs* (amplitude, variability and speed of both legs), *arms* (amplitude, variability and speed of both arms), and *central body* (amplitude, variability and speed, of the central body).

4.2.6 Dance ratings

27 women (aged 18-35) all currently enrolled on undergraduate courses took part in the dance ratings. They first viewed 15 seconds of each dance clip, presented using the methodology outlined in chapter 2. Immediately after each clip was presented, participants rated the clip they had just seen on perceived dance quality, masculinity and health using 7-point Likert scales (1 = low and 7 = high on a given attribute).

4.3. Results

4.3.1 Descriptive Statistics

Measures of central tendency and spread were calculated for each subscale of both subjective and objective health measures and are reported in table 5.

4.3.2 Female perceptions

Female perceptions of male dance movements showed high inter-rater agreement across all rating variables (Cronbach's alpha dance quality = .82; masculinity = .91; health = .95) and thus all subsequent analysis is based on mean ratings.

Table 5: summary of male participants scores on both subjective health measures in addition to objective measurements (unsigned symmetry, % body fat).

	Mean	SD	Std. Err	Median	Lower Quartile	Upper Quartile
BDI (Total)	6.36	6.14	.69	5	1.75	9.25
MHCC (Total)	13.54	6.60	.75	14	8	18.25
GHQ (Total)	1.97	2.65	.30	1	0	3
MHCC Indicators	8.47	4.81	.55	9	5	12
MHCC Immune Challenge	1	1.13	.13	1	0	2
MHCC Atopic	2.73	2.56	.29	2	0	4.25
MHCC Gastric	.41	.83	.09	0	0	.25
MHCC Fungal	.17	.41	.05	0	0	0
POMS Energetic-Tired	22.24	6.34	.72	23	18	26.25
POMS Confident-Unsure	23.06	6.49	.74	24	18	28
POMS Agreeable-Hostile	24.29	6.25	.71	25	20	29
POMS Clearheaded-Confused	24.87	7.35	.83	26.50	21	30
POMS Elated-Depressed	24.54	6.75	.76	25	20	29
POMS Composed-Anxious	23.09	6.09	.69	24	19.75	28
Resting HR	70.49	11.01	1.25	70.50	63.75	76
% Body Fat	20.33	9.59	1.09	19.50	14.88	22
Unsigned symmetry (Corrected)	.0214	.0123	.001	.02	.01	.02

Perceived dance quality and health were normally distributed (both NS K-S test result) however perceived masculinity was not. Table 6 shows correlations between rating variables.

Perceived dance quality was very highly correlated with perceived health which might suggest either that raters do not consciously differentiate between these questions or perceive the two to be linked. Masculinity however, showed much lower correlations with these

variables. When these were entered into a PCA, loadings for masculinity were very much lower on factor 1 (.58 compared to dance quality = .91 and health = .88) suggesting it may, to some extent, be measuring something different. Forcing a 2-factor solution (varimax) clearly showed this. Therefore, subsequent analysis will be based on perceived dance quality and masculinity only.

Table 6: Correlations between rating variables for female raters. Correlations with masculinity were analysed via Spearman's rho.

Female Raters	Perceived Health	Perceived Masculinity
Perceived Dance Quality	r = .76	r_s = .44
Perceived Health		r_s = .35

All $p \leq 0.03$

4.3.3 Perception of dancers and their subjective health measures

Correlations were then conducted between female ratings of dance quality and masculinity against subjective physical and mental health measures (questionnaires). Where non-normally distributed data was identified, Spearman's rho was used. Table 7 indicates that subjective health scores were unrelated to ratings of perceived dance quality or masculinity, many of them near zero, with the exception of a subset of MHCC questions regarding fungal infections. Of the twelve subjective health variables, only five were in the expected direction (negative) with perceived dance quality and six were in the expected direction with masculinity.

Table 7: Correlations between female perceptions and subjective health measures.

	Perceived dance quality	Perceived masculinity
BDI	r_s = -.067, p = .55	r_s= .04, p = .54
GHQ	r_s = .108, p = .37	r_s= .04, p = .73
MHCC Total ill health	r = -.06, p = .63	r_s= .06, p = .60
MHCC Indicators	r =-.20, p = .87	r_s= .06, p = .60
MHCC Immune challenge	r_s= .021, p = .86	r_s= -.11, p = .33
MHCC Atopic	r_s= -.120, p = .29	r_s= .02, p = .86
MHCC Gastric	r_s= -.119, p = .30	r_s= -.03, p = .77
MHCC Fungal	r_s=-.081, p = .48	r_s= .25, p = .03*
POMS Energetic-Tired	r = .-76, p =51	r_s= -.00, p = .97
POMS Confident-Unsure	r_s= .06, p = .89	r_s= -.28, p = .81
POMS Agreeable-Hostile	r_s= .14, p = .22	r_s= -.00, p = .98
POMS Clearheaded-Confused	r_s= .07, p = .57	r_s= -.02, p = .85
POMS Elated-Depressed	r = .07, p = .55	r_s= .04, p = .72
POMS Composed-Anxious	r = -.01, p = .96	r_s= -.06, p = .58

4.3.4 Perception of dancers and their objective health measures

Correlations were then conducted between female dance perceptions and body fluctuating asymmetry (FA), resting heart rate, blood pressure and % body fat. No significant correlations were observed between ratings of dance quality and objective health measures.

4.3.5 Biomechanical relationships with health measures

Despite health information showing no relationship with female perceptions of dance movements, correlations were finally conducted to establish whether there were any relationships between biomechanical variables (which can often be very subtle). Seven participants were removed from this analysis because of incomplete biomechanical data.

There were no significant relationships between any biomechanical variables and objective health measures. In terms of relationships between subjective health measures and biomechanical characteristics, very few significant relationships were observed. There was however significant positive correlations between movement of the central body and several subscales of the POMS mood questionnaire (agreeable/hostile r_s = .33, p = <.01; clearheaded/confused r_s= .24, p = .04; elated/depressed r = .35, p = <.01; composed/anxious r = .29, p = .01) as well as positive relationships between two subscales of the MHCC health questionnaire and movement of the legs (gastric r = .37, p = <.01; immune challenge r = .27, p = .02). These relationships appear to be universally in the wrong direction to what was predicted, in that greater movements of the central body were positively related to anxious, depressed and confused attributes of the POMS questionnaire; and greater movements of the legs were positively related to reported instances of gastric and immune problems. These relationships do not fit any notion of honest cues to health and caution must be taken with any implications made due to the number of correlations conducted (42 in total), which may yield Type 1 errors.

4.3.7 Biomechanical relationships and perceptions of dance quality and masculinity

Although no meaningful relationships were found between health measures, perception and biomechanical factors, the larger sample in this study will allow for the more powerful insight into what makes a good dancer and to establish whether the characteristics found in chapter 3 can be replicated. Table 8 shows significant positive relationships between perceived dance quality, and the arms and central body factors.

Stepwise regressions were then conducted to establish whether the arms factor was a more important predictor of dance quality rating.

Table 8: Correlations between perceptions of dance quality and masculinity, and biomechanical factors.

	LEGS	ARMS	CENTRAL BODY
Dance Quality	r = -.13, p = .27	r = .51, p = .<.001**	r = .32, p = <.01**
Masculinity	r_s= .12, p = .31	r_s= .18, p = .14	r_s= .09, p = .43

This was found to be the case when both the central body and arms factors were entered, only the arms factor was retained in the equation explaining 27% of the variance (R^2= .27, β= .51). As the predictors were different than in chapter 3, these significant relationships were then broken down into their constituent parts and regressed onto dance quality in order to establish the specific aspects of movement that were most important. Stepwise regression outputted a two variable solution explaining 32% of the variance with the variability of the left arm (β= .40) and size of the movement of the right arm (β= .25). This can be seen as support for the types of movement that are important in dance quality perceptions outlined in chapter 3.

4.4. Discussion

Through subjective assessments of male dancer's physical and psychological health as well as more objective FA and blood pressure measurements, the current study aimed to establish whether female observers could detect health based information from male dancers and to ascertain whether this information was mediated via the biomechanical variables outlined in chapter 3. The findings initially indicate that better rated male dancers are perceived to be healthier. However, analysis of female perceptions of dance quality and subjective/objective

health measures yielded no significant relationships suggesting females were unable to detect health information from male dance movements thus no mediation analysis was possible.

To establish whether health based information was actually encoded into male movements and was perhaps too subtle to be detected by raters, health measures were correlated with biomechanical factors known to be pertinent in female ratings of good and bad dancers. Whilst some subscales of the POMS mood and MHCC questionnaires were positively associated with movements of the central body, these were not in the expected direction. Together with the findings regarding larger, more varied central body movements being characteristic of good dancers in this study (as well as chapter 3), these relationships go against any notion of an honest cues hypothesis and suggests that these relationships may in fact be a result of type 1 error as there were many concurrent tests. Another possibility is that the relatively minor nature of the health complaints may not have affected movement enough to be visible in the short dance period.

In addition to subjective measures, each male participant had several bodily symmetry measures taken for assessment of developmental stability similar to that of Brown et al. (2005). Symmetry was analysed in accordance with Palmer (2004) controlling for trait size. FA is known to be associated with developmental stability and the robustness of genes from environmental pressures (e.g. Møller, 1992; Lens et al., 1999) although the extent to which it can be observed is debated (Swaddle, 1999). FA was thus used solely as a measure of quality rather than a signal. Results however indicated that such condition information was not encoded into male dance movements nor detected in female dance quality judgements. However, the nature of the majority of FA research in both humans and the animal kingdom is that it is extremely subtle and often effects are only observed with large sample sizes (>100). Cronbach's alpha revealed low reliability between the traits (after size correction) measured indicating that these measurement sites do not capture a centralised construct of

FA. Furthermore, the sample of males in the current study showed little variability amongst FA scores which might point towards a sampling issue.

Other more objective markers of health were similarly unconnected to either male dance movements or female perceptions. However measures of heart rate and blood pressure are influenced by a large variety of factors such as caffeine intake (Nurminem et al., 1999) and stress (Vrijkotte et al., 2000) that were not controlled for in this study and perhaps do not reflect health in a meaningful way. These findings seem to go against the hypothesis from the comparative literature suggesting that courtship displays convey condition information although several factors within in the study may explain the pattern of results observed. Firstly, this involves a relatively young, healthy sample of young men. Furthermore, the use of the BDI is typically used to assess clinical/severe depression and thus might not be the most sensitive measure of mild depressive symptoms in a mostly healthy sample. The Hospital Anxiety and Depression Scale (HADS) (Zigmond & Snaith 1983) might have been a better choice to assess mild symptoms, as it was developed to screen only for potential symptomology of anxiety and depression rather than provide a measure of the severity in clinical depression patients as the BDI is.

Further research regarding health-related hypotheses should ideally be undertaken using a broader sample of males (for example recruiting males whilst they have a cold) and getting them to dance for protracted periods of time which might allow for any issues to be highlighted in dance movements. This however might raise ethical considerations that might render such research impractical. Objective health measures such as immune challenge techniques could allow for more direct measurements of immunocompetence (Vedhara et al., 2006; Faivre et al., 2003) that circumvent the need for subjective ratings of current health status.

Questions pertaining to sexual selection in humans (including the current programme of study thus far) have assumed that signalling of information and its detection is mostly based on female preference (in essence inter-sexual selection). A recent paper by Puts (2010) however has challenged this hypothesis suggesting that many of the so called desired traits in men have evolved via intra-sexual competitions and thus should be assessable by other males for judgments of threat therefore subsequent studies in this thesis will employ males as raters.

In conclusion, the current study found no relationships to suggest that health information is encoded or detected by females in male dance movements. The current study however, employed questionnaires that may have been assessing quite minor complaints that may not have significantly affected movement, making differentiating between them negligible.

CHAPTER 5: STUDY 4, MALE MOVEMENTS AS POSSIBLE CUES TO STRENGTH AND PHYSICAL FITNESS

5.1. Background

In chapter 3, it was discovered that females displayed a consensus as to what constituted a 'good' and 'bad' dancer. Movements that were greater in variability and size, particularly of the upper body were key factors in female perceptions of male dance quality. However in chapter 4 it was discovered that female raters were unable to detect any relationships between dance quality and various psychological and physical health measures, nor with fluctuating asymmetry.

In various animal species, strength and fitness are believed to be assessed quite differently, using dynamic courtship displays, which are often elaborate feats of physical fitness, stamina, and strength. Both inter-sexual (Byers et al., 2010; Clark, 2009; Stiles, 1982) and intra-sexual (Byers, 1997) contexts have been reported.

Previous research involving humans has focused on dancing as a form of courtship display with researchers such as Hugill et al. (2009) finding that better rated male dancers had greater strength. However no such studies have investigated possible intra-sexual abilities in detecting strength via dance movements. Furthermore, research has not investigated whether cardiovascular fitness (another key component in both contests and resource acquiring abilities) can be assessed in male dynamic performances.

This study aimed to assess whether strength (upper and lower body) and cardiovascular fitness can be assessed in male dance movements in both inter-sexual and intra-sexual contexts, using the methodology outlined in chapter 2. Furthermore, it aims to explore whether these traits are related to any common biomechanical movements such as

those outlined in Chapter 2. It is hypothesised that movement speed could be related to dance quality as it may indicate vigour (Byers et al., 2010); and assuming the same criteria was used in the Hugill et al. (2009) and Neave et al., (2011) studies in the assessment of dance quality, upper body movements may be related to strength.

5.2. Method

5.2.1 Motion Capture & Stimuli Creation

The Vicon motion capture system was setup as outlined in chapter 2.

5.2.2 Participants(dancers)

Thirty males aged 19-37 (Mean= 23.6, SD= 4.9) participated in the study. All were paid £5 to compensate their time.

5.2.3 Objective strength and fitness measures

While actual VO^2max (the maximum amount of oxygen in millilitres, one can use in one minute per kilogram of body weight) is the standard in vascular fitness testing (Hyde & Gengenbach, 1997), several sub-maximal estimates of VO^2max have been found to be good overall correlates of actual performance, without the need for expensive gas-analysis equipment or maximal exercise. The Chester-step test is one such assessment and has been validated as a sub-maximal assessment of vascular fitness (Skyes & Roberts, 2004). A Chester step test is a progressively staged stepping task whereby participants are required to step onto and off a step in time with a rhythm (usually presented via CD) until they reach around 80% of their maximum heart rate (as calculated as 220 minus their age), or until they feel they cannot keep the beat. In order to measure heart rate, a Polar basic heart rate monitor strap and watch were used.

In order to measure upper body strength, each male provided one maximal force measure of handgrip strength (kg) on each hand (Takei Kiki Kogyo Grip Dynamometer). Following the protocol of Fink et al. (2007) the calculated mean of the left and right hand was used in the analysis (Cronbach's alpha = .94). To measure lower body strength a counter-movement jump was performed twice by each male. The jump involves a mat with a drawstring attached to a belt around the participant's waist. The objective is to move into a squat position and jump vertically using only the power of the legs for momentum with hands on hips. Jump height (cm) was used as the measure. This was performed using a Takei Jump MD vertical jump meter and the mean of the two measures ($r = .89$, $p<.01$) was used in the analysis.

5.2.4 Biomechanical analyses

In an attempt to ascertain possible mediators between dance perception and dancers' objective fitness, full-body biomechanical information was extracted from each dancer (Plug-In-Gait kinematic model, Vicon, Oxford). These were reduced by conducting factor analysis (PCA, Varimax). Based on the output of this factor analysis, a common structure emerged for the main structures of the body, thus the factors were integrated in the following way: sum of amplitude and variability for both arms explaining 57.67% of the variance (factor one: *arms*); sum of amplitude and variability for both legs explaining 12.34% of the variance (factor two: *legs*); and finally, sum of amplitude and variability for central body explaining 8.96% of the variance (factor three: *central body*). These mirror the important biomechanical characteristics and body regions previously reported (chapter 3).

In addition, a third factor emerged with high loadings for speed and duration variables, which showed opposite loadings. Because previous comparative literature (Byers et al., 2010) placed an emphasis on vigour (i.e. high speed movements), it was decided to drop the duration variables and sum the speed variables (factor four: *total speed*) for clarity.

5.2.5 Dance ratings

Twenty-seven women (aged 17-18 years), all in attendance at a North-East UK sixthform college, and 21 men (aged 20-33 years), all undergraduate students at a North-East University, took part in the dance ratings. Participants rated each of the 30 avatars on perceived dance quality, masculinity, strength and fitness using 7-point Likert scales (1 = low and 7 = high).

5.3. Results

In a first step analysis of whether dance quality ratings are related to dancers' strength and fitness was conducted. In a second step analysis of whether these relationships are mediated by biomechanical characteristics was conducted. Following Baron and Kenny (1986), the combination of two findings suggests mediation; i) biomechanical characteristics need to predict dancers' fitness/strength and ii) when dancers' fitness/strength is jointly regressed on quality ratings and biomechanical characteristics using the linear enter command, the strength of the relationship between fitness/strength and dance ratings declines.

5.3.1 Descriptive Statistics

In terms of the fitness and strength measures, mean handgrip strength was 38.4 kg (SD=10.1), mean $V0^2$max was 47.3 ml/kg/min (SD=10.1) and mean jump height was 40.2cm (SD=10.5). One-sample K-S goodness of fit tests and visual inspection of the data showed that objective strength and fitness measures were all approximately normally distributed (all $Z < .79$; all $p > .55$).

In terms of female ratings of dance quality, masculinity, fitness and strength, Cronbach's alpha revealed high inter-rater agreement across all rating variables (perceived dance quality = .93; perceived masculinity = .87; perceived fitness = .94; perceived strength = .91). Therefore all subsequent analyses were based on mean ratings. One-sample K-S goodness of fit tests and visual inspection of the data showed that all variables were normally distributed. Male ratings had similarly high inter-rater agreement across all rating variables (perceived dance quality = .91; perceived masculinity = .86; perceived fitness = .91; perceived strength = .9) and therefore all subsequent analyses are based on mean ratings.

Initially, separate analyses for female and male raters did not show any significant differences, and average female and male dance ratings were highly similar (r = .83). Therefore the two rating sets were combined. For ratings of dance quality, Cronbach's alpha revealed high reliability for the aggregated score (alpha = .96). Furthermore, aggregated perceptions of strength and fitness were very highly correlated with combined perceptions of dance quality (r = .91, r = .88 respectively) which might be as a result of raters not consciously differentiating between rating variables or perceive the variables to be linked, for clarity however these two measures were dropped. Masculinity on the other hand, showed a much lower relationship with combined dance quality (r = .60) suggesting it may, to some extent, measure something different. Male and female ratings of masculinity were quite similar (r= . 76) so the two rating sets were also combined (Cronbach's alpha = .75).

5.3.2 Perceived dance quality and dancers' objective strength and fitness

Correlations were conducted between perceived dance quality/masculinity and actual VO^2max, jump height and grip strength. Handgrip strength showed a significant positive correlation with dance quality (r = .40, p = .029) but neither VO^2max (r = -.18, p = .35 nor jump height (r = .08, p = .70 were significantly correlated with dance quality. Thus, better

rated dancers displayed greater upper body strength, but not lower body strength or overall cardiovascular fitness.

Perceived masculinity was significantly correlated with handgrip strength ($r = .46$, $p = .01$) and countermovement jump height ($r = .39$, $p = .03$) but not with VO^2max ($r = .34$, $p = .07$). Thus, more masculine rated dancers displayed greater upper and lower body strength but not cardiovascular fitness.

5.3.3 Biomechanics and perceptions of dance

Initially the four biomechanical factors were correlated with perceived dance quality/masculinity and objective fitness scores, the results of these are found in table 9. A pattern of results similar to chapter 3 emerged, whereby dance quality was positively correlated with movements of the central body ($r = .47$, $p = .01$) and the arms ($r = .54$, $p = .01$), specifically with regard to greater amplitude and variability of movements. Furthermore, better-rated dancers moved faster overall ($r = .36$, $p = .05$). Correlations between biomechanical factors and objective fitness revealed that males with higher handgrip strength also showed more movement (amplitude and variability) in the central body ($r = .40$, $p = .03$). Finally, males with higher estimated VO^2Max displayed slower dance movements overall ($r = -.55$, $p = .01$).

Of particular interest here is that both handgrip strength and dance quality are correlated with the central body factor which might be indicative that movements of the central body maybe mediating the previously reported correlation between dance quality and handgrip strength. When handgrip strength was regressed jointly on dance quality and on the central body factor, $\beta = .27$ ($p = .18$) for dance quality. This is substantially lower than the initial correlation of $r = .40$ [$r = .27$] and suggests that the observed relationship between perceived

dance quality and handgrip strength was partly mediated by the amplitude and variability of central body movements; the proportion of explained variance fell from 16% [7%] (unmediated) to 7% [2%] (mediated).

5.4. Discussion

The objective of the current study was to ascertain whether cardiovascular fitness and strength (both upper and lower body) could be detected in male dance moves by male and female raters. A further component to this study was to establish if any particular biomechanical variables were mediating these perceptions. It was predicted that stronger, physically fitter dancers would be perceived as 'better' by male and female raters. Overall it was found that better rated and more masculine rated dancers were indeed stronger as rated by male and female raters. In terms of biomechanical relationships, better-rated dancers displayed larger and more variable movements of their arms and upper body, as well as moving faster overall. Finally it was found that movements of the upper body somewhat mediated the relationship between strength and dance ratings. These findings are in accordance with research using static cues which suggests the face can signal strength (Fink et al., 2007; Sell et al., 2009), as well as dynamic research that has found positive associations between men's dance movements and women's perceptions of their dance quality (Hugill et al., 2009).

Cardiovascular fitness was not found to share any associations with dance quality ratings. Whilst this initially appears to go against previous literature that suggests cardiovascular fitness is observable in static facial photographs (Williams et al., 2000) and bodies (Hönekopp et al., 2007), such studies often mix strength based assessments ,so it may be that cardiovascular fitness is not the significant contributor to attractiveness in these studies. Another possibility is that the length of time men danced in this study was too short

to highlight their cardiovascular functioning. In the animal kingdom displays of vigour often occur over protracted periods of time (Byers et al., 2010) thus revealing cardiac endurance.

In addition, lower body strength did not show any relationship with ratings of dance quality. This is in accord with static research suggesting that lower body strength is not related with upper body strength (Sell et al., 2009). In Sell et al., (2009) the authors also noted that associations between lower body strength and attractiveness were not observed.

To conclude, the current study finds that men's upper body strength is being conveyed to both male and female observers via their dance movements. Biomechanically, dance quality is positively associated with greater amplitude and variability of both the central body and arms, and upper body strength appears to be conveyed by the variability and amplitude of movements of the upper body. Furthermore, movements of the upper body somewhat mediate the relationship between dance quality ratings and actual strength. Dance performance thus appears to provide information about certain aspects of male quality to both females and males.

CHAPTER 6: STUDY 5, MALE DANCE MOVEMENTS AS A POTENTIAL CUE TO AGE

6.1. Background

In Chapter 5 it was found that both male and female observers rated stronger men as better dancers. It was also found that larger, more variable movements of the arms and chest were the best biomechanical predictors of better-rated dancers. No associations however were observed for cardiovascular fitness and perception. That study also utilised a cohort of male raters, and while their ratings did not differ to those of the female raters, it raises the possibility that males are also sensitive to cues of strength. This provides some support to the hypothesis that intra-sexual selection maybe a driving force for selection of male typical traits (Puts, 2010) and that males are actively looking for cues to such traits to assess competitors at least as much as females (Sell et al., 2009).

Another trait of interest in both animal and human mate choice is female preferences for older men. From an intersexual point of view, older men typically have proven survival skills, which might point towards a robust gene pool (Buss & Schmidt, 1993). Older men also have traditionally been considered better mates because of their greater access to resources and thus, greater ability to provide (Betzig, 1986; Summers, 2005). In highly social creatures like many primate species as well as humans, age is typically positively associated with status and higher social rank resulting in greater access to such resources (Buss, 2004). In humans, female preference for relatively older men appears to be universal (Buss & Schmitt, 1993).

Contrastingly, the ability for males to gauge age in other males has not been explicitly investigated in humans from an intra-sexual viewpoint. Theoretically males might attempt to

seek cues pertaining to the status of other males, and age is thought to be a good correlate of such social standing (Hart & Piling, 1960; Alberts & Altman, 1995; Buss, 2004).

Aside from age being a positive correlate of social standing and access to resources however, post puberty serum testosterone is in steady decline over time, particularly in western cultures (Ellison et al., 2002; Feldman et al., 2002). This is attributed to a steady physical decline for example, reduced serum T has been linked to a lower quality of life, impaired sexual function, and lower bone and muscle mass (Travison et al., 2007). Furthermore circulating T levels have been suggested to have an impact on cognitive performance, particularly spatial tasks such as the mental rotation task (for example Shute et al., 1983) although often these studies are confounded by experience and learning factors and sometimes show curvilinear rather than linear relationships (Neave, 2008). Evidence from testosterone reduction therapies (in the treatment of prostate cancer for example) has also revealed that decline in serum T is related to negative performance outcomes on visiomotor solving, slower reaction times in working memory task and impaired hit rate on vigilance tasks (Salminem et al., 2004). This decline in T as a result of older age might result in males using age as a cue to the assessment of formidability and physical prowess.

The ability to gauge age via body movements has typically been investigated in clinical/biomechanical contexts (for example Samson et al., 2001). A study reported by Montepare and McArthur (1988) however suggests that when viewing point-light walks of people of varying ages, observers can quickly apply psychological characteristics to the walks such as younger walks were seen as more powerful and happy as a result of a more positive gait. Whilst this study found that raters were generally inaccurate when directly gauging age, they did find that age related characteristics such as masculinity (including dominance and physical strength), sexiness and happiness may be visible. This suggests that whilst age itself is not observable, movement provides information on condition and as age

increases, overall condition deteriorates (Samson et al., 2001). This may provide observers with an indirect correlate or cue to age based on condition of the movement.

This study therefore aims to assess whether age information is cued via male dance movements (as these may be more sensitive to gait differences than walking), and whether it can be perceived by male and female observers. Utilising the same methodology as outlined in chapter 2, a broad sample of ages will be recruited to dance. Furthermore, biomechanical factors will be extracted as in chapter 3 to establish whether specific factors may be influencing female perceptions as were found in chapter 4. Unlike previous studies in this thesis, it is hypothesised that perceptions of good dancers should be negatively related to the trait of interest, i.e. older men would be rated as poorer quality dancers.

6.2. Method

6.2.1 Motion-capture setup & stimuli creation

The Vicon motion capture system was setup as outlined in chapter 2.

6.2.2 Participants

Thirty male participants aged 18-65. As a result of incomplete biomechanical data, 3 participants were dropped from the analysis leaving 27 participants in the data set (mean age = 38.9; SD = 15.5; range = 47)

Forty female raters (aged 18-30, m= 20.93, SD= 2.94) all in attendance at Northumbria University, were recruited, each received course credit. In addition to this, 19 male raters (aged 20-38, m= 27.00, SD= 4.98) were recruited online to participate as a result of time constraints.

6.2.3 Biomechanical analysis

The biomechanical variables that were entered into a principal components analysis (varimax) for further reduction. Like previous chapters, results revealed the same pattern of factors for each body segment: factor 1; amplitude and variability of each arm, factor 2; amplitude and variability of each leg, factor 3; amplitude and variability of the central body, and factor 4; total speed.

6.2.4 Dance ratings

Participants were asked to rate perceived dance quality, masculinity on a 7-point Likert scale and provide an estimate of the dancers age in whole years between 18-65. For female participants this was presented in Empirisoft MediaLab 2008 (Empirisoft Inc., New York, USA) on a 15" laptop screen (1680x1050 resolution). Male participants were presented with a highly similar format of presentation whereby they saw each male dancer. Clip order was randomised for each participant. Clips were presented in a 640×360 (360p) pixel window on their personal computer and participants were asked to make a visceral judgement after they had seen each clip using sliders on the same 7-point Likert type scales. Whilst this resulted in a lack of control of participant focus and the physical dimensions of the video on their respective computers, the stimuli and scales used were the same.

6.3. Results

6.3.1 Descriptive statistics

In terms of female ratings of dance quality, masculinity and perceived age, Cronbach's alpha revealed reasonable inter-rater agreement across perceived dance quality and perceived age variables (.79 and .82 respectively). Perceived masculinity however showed much lower agreement (.59) suggesting raters may have found this question quite difficult and did not show a consensus.

In terms of male raters, Cronbach's alpha revealed that perceived dance quality and masculinity rating showed quite low inter-rater reliability (.51 and .42 respectively) whilst perceived age showed reasonable reliability (.73). This indicates that raters could not establish a consensus on good and bad dancers nor on masculinity. Due to the nature of the format that male raters were presented with, it is possible that a lack of interest in the study, the inability to control for participant focus on the task or control over video presentation size on different screens that is to blame for the poor reliability.

Tables 9 and 10 show correlations between all rating variables for male and female raters. Female raters appear to perceive better dancers as being younger but this is not related to ratings of masculinity. Male ratings on the other hand do not reflect this pattern, as perceived age did not influence their ratings of dance quality, but masculinity did, with better-rated dancers also being perceived as being more masculine.

Unlike other studies in this thesis, many of these variables are not strongly correlated with one another which is likely due to the low inter-rater reliability statistics for some of these variables.

Table 9: Correlations between rating variables for female raters.

Female Raters	Perceived Masculinity	Perceived Age
Perceived Dance Quality	r = .18	r = -.43*
Perceived Masculinity		r = -.20

* = Significant to .05 level

Table 10: Correlations between rating variables for male raters.

Male Raters	Perceived Masculinity	Perceived Age
Perceived Dance Quality	r = .61**	r = .13
Perceived Masculinity		r = -.21

** = Significant to .01 level

As in chapter 5, male and female ratings of dance quality were correlated with one another (Table 11).

Table 11: Correlations between male and female ratings.

	Male rated dance quality	Male rated masculinity	Male rated age
Female rated dance quality	r = .71, p = <.01**		
Female rated masculinity		r = .36, p = .07	
Female rated age			r = .21, p = .52

** Significant to .01 level

Table 11 reveals that only ratings of dance quality are significantly correlated with one another so further analysis also considers these as combined variables. Male and female

perceptions of masculinity and estimates of age appear to be independent of one another so it was deemed appropriate to keep them separate.

Perceptions of age and their relationship with actual age

In terms of female perceptions, perceived masculinity was significantly negatively correlated with the actual age of the dancer ($r = -.59$, $p = <.01$) suggesting that dancers who were rated as masculine were actually younger. No significant relationships were observed between perceived dance quality and the actual age of the dancer ($r = -.14$, $p = .50$) nor direct perceptions of age and the actual age of the dancer ($r = .14$, $p = .49$).

In terms of male raters, no significant relationships were observed between perceptions of dance quality or masculinity on the actual age of the dancer ($r = .05$, $p = .79$, $r = -.21$, $p = .29$ respectively). A strong positive relationship was observed between male raters direct perceptions of age and the actual age of the dancer ($r = .54$, $p = <.01$). In other words, older dancers were rated as being older.

The combined dance quality variables (male and female ratings of dance quality combined) similarly reveal no significant relationships with the dancers actual age ($r = -.26$, $p = .89$).

Biomechanical relationships

Next, significant relationships between perceptions of dancers and actual age were then correlated against the four biomechanical factors in an attempt to ascertain particular characteristics that may be influencing perception (i.e. may be functioning as mediators).

Firstly, simple correlations were conducted between the actual age of the dancer and the four biomechanical factors (Arms, Legs, Central body and Overall speed) to determine

any trends in the way they actually moved. It was found that no significant relationships were observed (Table 12). This suggests that age is not related to distinct biomechanical trends.

Table 12: Correlations between actual age and the four biomechanical factors.

	Total Speed	Arms	Legs	Central Body
Dancers Actual Age	r = .17, p = .41	r = .36, p = .07	r = .32, p = .11	r = .02, p = .93

In terms of female rated masculinity (which saw a negative relationship with the actual age of the dancer), significant negative correlations were observed with the arms factor (r = -.55, p = <.01), legs factor (r = -.69, p = <.01) and overall speed factor (r = -.51, p = <.01) but not the central body factor (r = .16, p = .43) suggesting that more masculine rated dancers danced more slowly overall, and showed less amplitude and variability in the movements of their arms and legs.

In terms of male perceptions of age (which showed a significant positive correlation with the dancers actual age), a significant positive correlation was observed with the arms factor (r = .56, p = <.01) suggesting that dancers perceived to be older showed more amplitude and variability of their arms. No relationships were observed between the central body (r = -.23, p = .27), legs (r = .24, p = .25) or speed factors (r = .26, p = .20).

6.4. Discussion

The objective of this study was to ascertain whether the age of a male was encoded into his dance movements.

It was found that females perceived ‘good’ male dancers to be younger but this was unrelated to the dancer’s actual age. This initially suggests that whilst age may not be

considered directly, age's effect on condition might be. The finding that dancers rated as more masculine were in fact older also indirectly supports this suggestion as it follows the trend of T's decline with age, because T has positive effects on the musculoskeletal system and muscles (Hugill et al., 2009; Cardinal & Stone, 2006).

In terms of male ratings, a strong positive correlation was revealed between male ratings of dancer age and the actual age of the dancer, suggesting that age was more observable for males. However, as male ratings suffered poor inter-rater reliability, possibly due to the online format, this finding should be treated with caution.

Biomechanically however, no relationships were observed between older and younger dancers on the characteristics extracted. This suggests that older men did not dance significantly differently from younger men, which might suggest possible limitations to the biomechanical movement variables (duration, speed, amplitude and variability) in that they could describe movement too generally. An alternative suggestion might be that the older males who volunteered did so because they were very fit for their age and they could thus reflect a biased sample of older males.

In conclusion, the findings of this study in relation to female ratings follow the trends in previous studies whereby age cannot be directly observed but characteristics pertinent to age can be applied them. Younger men were perceived to be better dancers, and dancers perceived to be more masculine were actually older, which follows the trend of circulating T levels. Male raters on the other hand were able detect the age of dancers in some way but biomechanical relationships did not account for such an ability. Biomechanical differences were not observed between older and younger dancers, which may point towards limitations in the sensitivity of such general measures.

CHAPTER 7: GENERAL DISCUSSION

7.1. Overview of studies and literature

The aim of this thesis was to explore whether male dance was providing female observers with cues to his physical and psychological condition, whilst addressing the issues of static and structural confounds. In using a 3D optical motion capture system it was also possible to extract quantitative kinematic data (biomechanics) with great accuracy, allowing for the analysis of individual movement characteristics that could be linked with certain male traits as possible mediators. The following studies and their basic findings are outlined below.

Study 1 (Chapter 2) established a reliable and robust method in which to record male dance movements with great accuracy, and apply a realistic form (avatar) in which to present to female observers. In order to test its viability, a standard sex identification task was employed which has previously shown robust findings in perceptual research (Troje 2003). Findings indicated that this method allowed for very accurate perceptions of sex, suggesting that the use of an avatar had no detrimental effects on perception. The subsequent experimental studies used the same avatar technique throughout.

Study 2 (Chapter 3) addressed the question of what makes a good male dancer as rated by female observers. In an attempt to answer this question, 37 females rated 15 second dance clips of 19 men. From each dancer, kinematic information was extracted and correlated with female perceptions. It was found that better rated dancers showed larger and more variable movements of the upper body, as well as moving their right knee faster.

Study 3 (Chapter 4) aimed to ascertain whether health and condition-related information is conveyed via dance moves to female observers (subjective health and FA

measures) and whether these were in any way related to biomechanical characteristics, in particular the ones outlines in experiment 2 (chapter 3). Contrary to expectation it was found that the current health status of the male was not associated with his dancing ability, neither through subjective questionnaire measurements, nor more objective measurements of FA. It was concluded that the low variability in health data outlined in the questionnaires may have precluded its detection in dance movements or the relatively acute nature of the health complaints in questionnaires might not have significantly affected movements.

Study 4 (Chapter 5) investigated whether physical strength and cardiovascular fitness were cued via male dance movements. Based on a recent paper by Puts (2010), instead of just investigating this from an intersexual point of view (by using solely female observers), a group of male observers were also recruited to investigate if they too could detect the strength and fitness of a dancing male, which might point toward intra-sexual signalling. Furthermore biomechanical facets were also extracted which might point towards particular movements mediating such cues. It was found that better dancers (as perceived by both male and female raters) displayed greater upper body strength, but not lower body strength or cardiovascular fitness. This study also found that larger, more variable movements of the arms and upper body as well as faster overall movements were indicative of good dancers, findings that are similar to those in study 2. Dancers' strength measures were also correlated with larger, more variable movements of the upper body, which suggests that the biomechanical makeup of each dancer at least partially mediates the relationship between observer's perceptions of dance quality and objective strength.

Study 5 (Chapter 6) continued the multidimensional approach from Experiment 4 (intra and inter sexual) to investigate whether age could be detected in male dance movements as this should have an effect on locomotion. Again, like the previous study, age is a trait of interest to both males and females and so male raters were also recruited.

Furthermore biomechanical facets were also extracted which might point towards mediation. Female perceptions were unrelated to the actual age of the male dancer, suggesting that age may not be encoded into dance movements. Female raters did however perceive better dancers to be younger, and the actual age of the dancer was negatively correlated with the masculinity rating given by female raters. Male perceptions of dancers' age, however, were positively correlated with the actual age of the dancer.

The main driving force behind this thesis is sexual selection, in particular the traits implicated in solving adaptive problems that have arisen as a result of our evolutionary heritage. Much of the work on mate choice in humans has centred on the role of intersexual selection, in particular female mate choice. This is derived from the notion that females are the 'choosers' of mates as a result of their increased parental investment (Trivers, 1975). This apparent choice is thought to have led to the development of a variety of conspicuous ornaments and structures in males that are clearly a burden to the survival of the male and have been developed at great physiological cost. Theorists such as Zahavi (1975) and Hamilton and Zuk (1987) discounted the original supposition that these ornaments simply develop as a result of a runaway process (Fisher, 1935) and hypothesised that they have a more significant value, to 'honestly' signal information about the genetic/physical condition of the male. Many traits are preferred because of their adaptive benefits such as health, and the ability to dominate other males to control the flow of resources. Such traits are not always directly observable, but must be inferred in some way, generally via ornamentation and physical condition. As females could pay dearly as a result of male deception, females should evolve the cognitive mechanisms to enable them to differentiate between genuine and fake cues. They therefore look for honest signals that are difficult to fake, and this explains why many of these ornaments are a great handicap to males (Hamilton & Zuk, 1987, Zahavi, 1975; Gangestad & Thornhill, 1997; Bradbury & Vehrencamp, 2011). Only males of genuine

genetic/physical quality can initially develop the ornaments, and then maintain them in spite of physiological cost.

One often-overlooked avenue of potential signalling value is dynamic cues. The animal kingdom is full of examples of how females observe and assess the complex feats of vigour and skill of males as a means choosing a mate (Byers, 1997; Byers et al., 2010; Clark, 2009; Barske et al., 2011). The principal benefit of using movement as an assessment tool is that it is very visual and conspicuous. An additional benefit is that the ability to move in a vigorous and skilful way requires the use of many of the bodies' systems such as the nervous, musculoskeletal and cardiovascular systems, which in essence makes movement an honest cue, as these displays are often performed at intrinsic limits (e.g. Clark, 2009). Rather than movement being classed as a signal (which would suggest it has developed specifically for the purposes of advertising quality), movement clearly did not develop for this purpose but still honestly conveys condition-dependent information, and so it is classified by definition as an honest cue (Bradbury & Vehrencamp, 2011).

In humans however, research of this kind is still in its infancy in the realm of sexual selection, despite movement having received much attention in the visual perception and neurological domains, using novel methodologies to reduce the visibility of static cues known to influence people's perceptions. Research concerning the role of movements in sexual selection is still lacking, despite Farnell (1999) highlighting this lack of research over ten years ago. It is known from the field of perception that humans are very adept at identifying basic and higher order aspects of information, (such as sex, emotional state, and intent) from sparse kinematic cues presented for very short periods of time (Runeson & Frykholm, 1983; Dittrich et al., 1996; Brownlow & Dixon, 1997).

Based on the definition of courtship displays in the animal kingdom, researchers have begun to question whether human dancing is similarly used by females to assess a male's physical condition. Dancing is seen as creative, expressive, communicative, and centres around sexuality (Kaeppler, 1978; Hannah, 2010). Indeed some evidence suggests that male dance informs female observers about his strength (Hugil et al., 2009), and ratings of dance quality are positively related to prenatal T exposure (Fink et al., 2007). However this research has been conducted using Gaussian blurred videos that result in very degraded stimuli, and the height and build of the person still 'leaks' through in the resulting video. By using a 3D motion capture suite and animation software to control for height and build, Brown et al. (2005) attempted to link dance movements to physical condition (via comparisons with FA). The technique used was exceptionally good at keeping motion cues pertinent whilst eliminating confounding variables, however their findings were found to be fraudulent (Trivers, 2009).

7.2. Do male dance movements provide cues to reproductive quality?

The novel findings reported in this thesis do indicate that male dance movements provide some cues as to the reproductive quality of the male, and such information is provided to both females and males. Most of the previous literature has employed an inter-sexual perspective to the investigation of cues and signals whereby males were assessed by females on their apparent reproductive quality. This thesis initially followed this perspective by using male dancers being rated by female raters on dance quality and masculinity. Based on the work of Fisher (1930) and later Zahavi (1975) and Hamilton and Zuk (1982), female mate choice drives the development of conspicuous ornaments that would otherwise be eliminated by natural selection because of the handicap they exert on the male. It has been hypothesised that

these ornaments are preferred by females because they signal or cue information to other desired traits that are not directly observable but are important in reproduction, protection and offspring prosperity. This has resulted in a wealth of research concerned with identifying ornaments, what they signal, and whether they lead to increased reproductive success. Research investigating signals has often explored them based on attractiveness (in particular the face).

Thus, a key question in this thesis was to explore what dance movements are considered attractive to females. The results indicate that there is a general consensus among women about male dance quality, and the extraction of biomechanical characteristics that describe dance were on the whole successful. By extracting kinematic data from each dance, it was revealed that the key predictors of perceived quality were amplitude and variability of the upper body (trunk and neck) as well as speed of the right knee. In a more salient context, better dancers showed greater twisting of their chest and shoulders whilst moving their right leg (possibly because they were standing on their non-dominant leg).

Hannah (2010) stated that from an anthropological perspective, dance in humans is considered to be an important aspect of mate attraction, as well as an expression of sexuality, and so these larger, more variable movements might form the basis of attraction, and perhaps express traits relevant for sexual selection in men. Comparative literature suggests that male motor displays (particularly vigorous and skilful movements) may provide valuable cues of physical condition to females that are impossible to fake, thus making them ideal for the assessment of mate quality (Byers et al., 1994; Byers et al., 2010). In the past 10 years, some researchers have begun to apply this supposition to human dance with some success: Brown et al. (2005) found a relationship between male dance moves and body fluctuating asymmetry (a marker of developmental stability) but didn't speculate as to its relevance in mate selection. More recently, dance has been suggested to be linked to a man's underlying PT

exposure which is thought to underlie many male sexual traits (Fink et al., 2007) as well as a cue to his physical strength (Hugill et al., 2009).

The movements outlined in this study, particularly those of speed and amplitude, fit well within the notion of vigour. Movement skill however is somewhat more subjective and the general biomechanical characteristics extracted do not capture skill in the same way that vigour can. Female participants did however share a consensus of a good dancer and this question likely implies that skill is involved. The finding that variability plays a role in female preferences of good dancers is likely because a monotonous movement is less interesting to watch.

It is known that female animals pay close attention to courtship movements in order to gain cues as to the genotypic and phenotypic quality of the male (Houle & Kondrashov, 2002). Researchers have therefore begun to focus on movement as a possible signalling mechanism in humans. Thus far, positive relationships have been found between men's dance movements, strength and symmetry (Hugill et al 2009; Brown et al., 2005). Reliable estimations of physical strength (especially upper-body strength) can also be extracted from male facial characteristics (Fink et al., 2007; Sell et al., 2009) and so the human face/body may be acting as a condition-dependent ornament of certain aspects of male quality (Fink et al., 2010). Study 3 (chapter 4) sought to investigate whether health and developmental stability (both key characteristics in good mating choices) are encoded into male dance movements. However, health information was found not to be encoded in male dance, though it is suspected that the questionnaires used reflected rather minor health complaints that may not have significantly affected movement, especially given the short performance time of 30 seconds. In addition, no relationships between dance quality ratings and the FA of the dancer were observed. This is in contradiction to the Brown et al. (2005) research but as this work

was later shown to be fraudulent (Trivers, 2009) it could be that in a normal population FA may not be related to dance quality.

It has often been considered that in human mate choice, females are the driving force in the development of male cues and signals (e.g. Buss, 2004; Miller, 2007). However more recently this directional hypothesis has been challenged by Puts (2010) who argues that the strongest forms of selection occur in intra-sexual contexts as there is only one winner (for example fights for access to females, sperm competition). Past research into male weapons (such as antlers or condition of canine teeth in primates) for example has revealed that other males use the appearance of these structures in order to assess formidability, dominance and overall condition (Bower, et al., 2001; Manning & Chamberlain, 1993; Troisi et al., 1990). In humans too, a male's fighting strength (upper body strength) can be gauged by both men and women (Sell et al., 2009). Based on this it may be logical to presume that males could be using another male's dancing to gauge potential competition. In study 2 (chapter 3) it was found that the upper body is in some way important in people's perceptions of good and bad dancers and in the current study the arms were particularly characteristic of good dancers. Upper body strength from both the chest and arms is indicative of the ability to inflict damage to an opponent, and this is thought to be as a result of intra-sexual competition thus explaining why such large differences are observed between men and women in upper body muscle mass. The remaining studies in this thesis therefore also utilised male raters in order to investigate these hypotheses further.

Study 4 therefore sought to investigate whether strength and physical (cardiovascular) fitness are cued by male dance moves and could be detected by female and male observers. In humans, reliable estimations of physical strength (especially upper-body strength) can be extracted from male facial characteristics (Fink et al., 2007; Sell et al., 2009; Windhager et al., 2011). Positive relationships have also been found between men's dance movements and

their actual physical strength (Hugill et al., 2009), and so the human face/body may be acting as a condition-dependent ornament of certain aspects of male quality (Fink et al., 2010). The extent to which men's dancing provides cues to his strength to other men has yet to be investigated. Whilst some studies report that cardiovascular fitness can be detected in static images of bodies (but not faces; Hönekopp et al., 2007), research to date is yet to explore whether cardiovascular fitness is encoded into dynamic displays.

Significant positive correlations were found between male hand grip strength and perceived dance quality and masculinity, such that males with greater upper body strength were also rated as being better dancers and more masculine. This finding is in accord with a previous study reporting that male dance is associated with grip strength, despite different methodologies (Hugill et al., 2009) and supports the notion that both men and women have evolved cognitive adaptations for the visual assessment of strength from men's faces, bodies, and movements (Fink et al., 2007; 2010). However, it cannot be acknowledged that these results in themselves can be interpreted in terms of different mating strategies (i.e. female preferences vs. male competition) as males and females were only asked for their initial assessments of dance quality/masculinity. In order to address this question in more detail, future studies could ask females for example about their preferences for dating such males, while males could be asked their perceptions of the dominance and/or fighting ability of the dancers.

No relationships were found between lower body strength (jump height) and perceived dancing ability. This is initially puzzling as one would perhaps expect that upper and lower body strength would be providing the same information to an observer and especially for dancing ability we expected that lower body strength would form a useful assessment. Previous research by Sell et al. (2009) also noted this discrepancy, in their study,

upper body strength could be accurately determined from facial photographs; yet lower body strength could not. They also found that perceived fighting ability was strongly associated with upper body strength, and concluded that this ability to discern upper-body strength is principally because men are looking for cues of 'formidability' in other males who may be potential rivals. Upper body strength is highly related to fighting ability as it reflects the ability to do damage especially in intra-sexual conflicts, and the ability to gauge strength before potential conflicts is sensible, especially to other males (see also Muñoz-Reyes et al., in press). This supports the argument of Puts (2010) who explains that upper body strength and associated conflict traits such as size, aggression and dominance primarily evolved via intra-sexual conflicts with other men, rather than via inter-sexually like many researchers assume. However, as we did not ask the male raters to judge the male dancers on their perceived fighting ability, this cannot be confirmed. Relationships were however found between perceived masculinity and lower body strength in that more masculine rated males also showed greater lower body strength. Whilst this finding is contrary to the findings of Sell et al., (2009), masculinity itself is often associated with muscle mass which might be why this is associated with masculinity rather than dance quality.

One element of courtship displays that appears to be of particular significance is that of vigour; male animals that can engage in highly-energetic displays are providing the female with cues to their condition and overall quality (Darwin, 1871; Byers et al., 2010; Fusani et al., 2007; Barske et al., 2011). Physiologically, displays of vigour over long periods of time rely upon good cardiovascular fitness, which is a good sign of overall health. This view is supported in this thesis as the speed at which a male danced was positively related to their dance quality rating. However, whilst one might hypothesise that such displays may be related to cardiovascular fitness and used as an honest cue to condition, this was not found to be the case in this thesis as cardiovascular fitness was negatively related to speed of

movement and not related to dance quality ratings. Dance performance time may have played a significant role in this finding.

A final study sought to investigate whether age was detectable in some way via male dance movements. From an evolutionary perspective the ability to gauge age stems from its negative relationship with physical condition. Females should be looking for males in good physical condition but this is a trade-off because older men typically have greater access to resources and financial prospects (Buss & Schmidt, 1993; Buss, 2004). Research tends to suggest however that women tend to marry men only slightly older than themselves (around 3-5 years; Buss & Schmidt, 1993). In terms of dance quality ratings in this study, females perceived the best dancers to be younger which somewhat supports the notion that dance may be able to convey physical qualities to females, so one might not expect to see a positive relationship. However female perceptions of male dance quality were not related to the actual age of the dancer, suggesting that age may not be considered in dance movements directly, but rather its effect on condition can be. This is also somewhat indirectly supported by the finding that female ratings of the masculinity of the dancer was in fact negatively correlated with the dancer's actual age (supporting Montepare & McArthur, 1988). Testosterone (T) a key factor in physical and behavioural masculinisation especially in males (Fink et al., 2007; Neave, 2008) is known to have positive effects on the musculoskeletal and nervous systems and has anabolic effects on muscle mass (Cardinale & Stone, 2006; Hugill et al., 2009). At puberty, circulating T levels steadily rise until around early/mid-twenties where it reaches a peak and then steadily declines with age (Feldman et al., 2002). This, coupled with the finding that females rated younger men as more masculine, raises the possibility that T may be influencing condition, and is reflected in dance movements, although this remains speculative at this stage.

Because of its negative relationship with physical condition, age should be a trait of interest for other males, and movement might be used in addition to other cues of physical condition that can be assessed via other mediums such as the face to reduce possible uncertainty. From an intra-sexual point of view, the ability to accurately gauge the formidability and condition of other males is important for the avoidance of harm during conflicts (Sell et al., 2009; Puts, 2010). It was found that male raters' direct perceptions of the age of the dancer were positively correlated with the actual age of the dancer, suggesting they could discern age from such movements, thus supporting this perspective.

Despite this correlation between male rating of age and the actual age of the dancer, the biomechanical characteristics extracted did not establish any trends between the way older and younger men danced. Given the evidence that physical ability and condition decline with age and this has a negative effect on movement (Samson et al., 2001), this suggests possible limitations to the characteristics extracted in detection of quality.

Overall, this thesis found that condition dependent information was encoded into dance quality and unearthed the possibility that male dance movements provide cues to both men and women. However it did not explore the key question of which selection pressures lead to the development of such cues from dance movements (i.e. whether inter or intra sexual selection). Much of the previous literature seems to only consider the view that female choice has formed the development of ornaments as signals/cues to condition (e.g. Buss, 2004; Miller, 1998). However, Puts (2010) argues that mate choice (intersexual selection) may not be the primary mechanism in sexual selection. Instead of the popular viewpoint that cues and signals in males are detected by females to make mate choice decisions, many male typical traits favour selection via intra-sexual conflict such as physical prowess, athleticism, weapons (e.g. antlers) and aggression. Contests, whereby threats or acts of violence fully exclude other males' access to mating opportunities creates a more clear-cut mechanism of

directional selection because the outcome of such conflict is very decisive, and winners completely exclude other parties. A principal example of this is in sperm competition whereby only one is successful and so only the winner's genes are passed on. Thus, this perspective and evidence from this thesis provides a viable avenue of future research that should attempt to tease apart this argument by asking females about their preferences for dating, and ask males questions based on dominance (e.g. Mueller and Mazur, 1997) and potential fighting ability (Sell et al., 2009).

7.2.1 How does dance fit into evolutionary theory?

There is a well-established research base concerning static cues and mate assessment in humans and this thesis has extended these findings to show that certain dynamic movements also play a significant role in providing information about certain relevant attributes. This provides support for a 'multiple cues hypothesis' (e.g. Møller & Pomiankoski, 1993) in humans. However there are several hypotheses as to whether the use of multiple cues provides information on different mate-qualities (multiple messages hypothesis) or common mate-qualities (Johnstone, 1996). The reason why the same trait may be advertised via multiple modalities is because it is thought that, to some degree at least, signals may not be a 100% accurate representation of the trait of interest (i.e. error in signalling), this is also known as the 'redundant signalling hypothesis'. Whilst empirical support is provided for both arguments (for a review, see Candolin, 2003), the results in this thesis provide some support for the redundancy hypothesis because physical strength and age for example can also be detected in static pictures of faces and bodies (e.g. Sell et al., 2009). The use of multiple cues in this way may be used to produce more accurate decisions and to reduce receiver uncertainty as this brings obvious mating benefits (Sell et al., 2009). In addition to this, the

use of so-called ‘back-up cues’ makes it more difficult for the sender to deceive the receiver with dishonest information (i.e. makes it much more difficult to ‘cheat’) as research suggests that, at least to some degree, dishonesty is expected in signalling systems (Dawkins & Guildford, 1991). A further component of this hypothesis is that it allows for receivers to expend less time and energy investigating senders if a trait is presented via multiple modalities, and also facilitates the detection of differences between two similar potential mates. However whilst the results in this thesis regarding cues to physical strength and age have also been found to be detectable in static modalities, it is unknown whether receivers of such signals use both modalities in order to reduce error or use one over the other, thus providing an avenue for future research similar in nature to Sell et al. (2009).

7.3. Study Limitations and Future Directions

Throughout this project, several methodological constraints have become apparent. Many of these stem from the preliminary and novel nature of the technique used for recording movement and the procedures. As a result, the scope for future research is broad.

Firstly, a general issue arose in all studies in this thesis that could not be remedied. Occasionally, the avatar on the point-light skeleton was a poor fit. The avatar was of standardised height and build, and could cope well with the majority of optical data from Vicon. However participants who were particularly short (i.e. five feet and below) caused problems with limb articulation thus creating an unnatural looking representation. This data was typically dropped from analysis because of this anomaly.

A further issue stemmed from the amount of time each male danced for. Initially, the 30 second performance period was informed by the amount of time for participants to get settled into the system and to record a feasible amount of data. However findings from studies pertaining to health and physical fitness raised the possibility that this may have been too short. In the animal kingdom, feats of vigour (in ungulates for example, Byers 1994; 1997; Hebets & Uetz, 1999; Byers et al., 2010) can take place over extended periods of time thus showcasing the male's stamina, endurance and cardiovascular capabilities. If the performance time was extended and perhaps the latter aspect of a males dance shown to observers, or if participants exercised to a state almost reaching exhaustion, and then danced for 30sec, these traits may become more apparent, allowing observers to discern with greater ease.

An important limitation stems from the inability to time lock rhythm onto stimuli for presentation to raters. Rhythm and the ability to keep a beat are key components in the dance aesthetic and the two are inextricably linked (Wallin et al., 2000). This is thought to be a by-product of vocal mimicry (essentially the ability to learn language skills) and thus an explanation of why music always accompanies dance (Patel, et al., 2009; Schachner et al., 2009). Whilst male dancers were always presented with the same rhythm (a 125bpm, drum beat), they each started their dances at different times (when they were ready). Also, whilst typically the middle 15 seconds of each dance was extracted to Autodesk Motionbuilder, this would represent a different point in the drum track thus making it impossible to perfectly align rhythm post-hoc. Furthermore, it was not possible to analyse the dancer's time keeping performance with the available equipment. Because of these issues, it was deemed appropriate to exclude the rhythm track from raters. Presumably, information regarding the coordination of a male dancer should better reveal his physical condition, and give raters greater confidence in their decisions if the rhythm is presented alongside the performance.

Other methodological issues arose from the choice of data extraction. In the age study (experiment 5, chapter 6), it was found that the biomechanical characteristics that were extracted from each males dance (amplitude, variability, speed and duration) were not sufficient to significantly differentiate between older and younger dancers. The literature on the subject of age (e.g. Samson et al., 2001; Travison et al., 2007) suggests that physical condition deteriorates with age and thus affects gait. The reason for choosing general measures of amplitude, variability, speed and duration of movement in the first instance was because of the highly preliminary and novel nature of this research but Vicon Nexus allows for virtually limitless movement characteristics to be extracted, so choice of what movement data to extract is a key consideration.

A further note is the use of correlational design employed in all studies. Because of the large amount of biomechanical characteristics in particular, one needs to exercise caution when interpreting such correlations in order to avoid false positive results (error of the second kind). This would typically be addressed using Bonferroni corrections or similar. However, due to the magnitude of most data concerning subtle cues of condition (such as symmetry & PT) being relatively small, using Bonferroni corrections might be too stringent in this case. In addition to this, results appear to support both previous comparative (Byers et al., 2010) and human literature (Hugill et al., 2009; Neave et al., 2011). In future studies, larger sample sizes and more precise targeting of biomechanical variables of interest will combat this issue.

Sampling issues must also be highlighted here. Studies in this thesis required volunteers to do potentially embarrassing things they typically would not do whilst be watched (never mind recorded), only a certain type of person who was reasonably confident was likely to volunteer (i.e. a certain personality). Many gait perception studies report that characteristics such as emotion (Pollick et al., 2001; Atkinson et al., 2004) and intent (Runeson & Frykholm, 1983) are accurately detected in gait. These studies suggest that many

attributes about the person are encoded into their gait (Bull, 2001), which raises the possibility that personality-based characteristics are also presented in the dances of others. From the outset, this thesis revealed that amplitude (size) and variability were important characteristics of a good dancer and these movements may be indicative of certain personality traits such as extraversion. In point-light walkers this has found to be the case (e.g. Heberlein et al., 2004; Ambady & Rosenthal, 1992) and a preliminary investigation by Fink et al., (2012) has found that conscientiousness and agreeableness are positively associated with women's perceptions of male dance movements. Whether these traits have biomechanical underpinnings, or how important they are in predicting dance quality ratings remains unknown, thus forming a strong rationale for future studies.

In rating studies, female raters' judgements were sought in order to establish evidence for inter-sexual selection. However, their stages in their menstrual cycle were not controlled for. Female preferences for certain male characteristics have been found to fluctuate throughout the menstrual cycle. It is hypothesised that females become more attentive to markers of physical condition during the most fertile (follicular) phase of the cycle (Penton-Voak & Perrett, 2000) and make decisions of quality that they do not make at other times (e.g. preferring the scent of men with low FA; Gangestad & Thornhill, 1998). Jones et al., (2005) reported that health and condition-related benefits are of higher interest during fertile phases of the menstrual cycle, whereas investment-based cues are preferred during the non-fertile phases, which results in females showing a decreased preference for feminine faces during high fertility. Penton-Voak and Perrett (2000) report that exaggerated T-related facial features (i.e. a more masculinised face) are preferred during the fertile phase of the cycle than during non-fertile phases. Highly masculinized faces are generally not found to be the most attractive in the majority of studies that digitally manipulate such features because such faces are thought convey negative social characteristics such as aggression (Mueller and Mazur,

1997; Perrett et al., 1998) and an unwillingness to invest (Fink & Penton-Voak, 2002) despite this being a signal of health (Rhodes et al., 2003). Penton-Voak and Perrett (2000) concluded that females prefer more exaggerated masculine traits during high fertility because of heightened sensitivity to characteristics that are thought to reveal physical condition, and T is thought to be an immunosuppressant, and thus is an indicator of physical condition (Folstad & Karter, 1992). This preference for masculinisation has also been both replicated (Little et al., 2008) and extended to voices (which are known to be influenced by T) with females during fertile phases preferring deeper voices (Feinberg et al., 2008). Controlling for menstrual cycle effects has received virtually no attention with regard to perceptions of gait quality in the context of sexual selection. However a recent paper by Zwan and Herbet (2012) controlled for such effects. The authors presented male and female walkers in point-light format to females during peak fertility and non-fertility phases of the menstrual cycle. The walkers were altered to show slight gait asymmetries and it was predicted that during peak fertility females would prefer the symmetrical gaits because this would be indicative of physical condition. Contrary to prediction, the authors found that preferences of low and high FA gaits did not change over the menstrual cycle; however fertile females showed fluctuations in the rating of female walkers over the cycle. During high fertility, female observers showed a marked decline in rating of female walks compared to the rating of the same walks in their non-fertile phase, which supports the pattern of results found in previous studies involving the femininity of faces over the menstrual cycle (Jones et al., 2005). Overall, this pattern of findings reveals that any mate choice related questions would profit from taking into account menstrual cycle phases when using female raters.

Another avenue that would directly extend the current body of research is that of sexuality. It has been proposed that sexual orientation in humans is somewhat influenced by prenatal sex hormone exposure (often measured via 2D:4D) however research appears mixed

with some reporting that homosexual men have lower finger length ratios (higher exposure to prenatal T) than heterosexuals (Manning, 2000), possibly as a result of the fraternal birth order effect (Rahman & Wilson,. 2003); while some studies report higher ratios (Lippa, 2003) and some report no relationships between 2D:4D and sexual orientation (Williams et al., 2000). Homosexuals are also reported as showing opposite-sex patterns of height and weight (Bogaert & Blanchard, 1996) and occupational interests (Bailey & Zucker, 1995). Evidence also suggests that sexual orientation can be judged via short dynamic gait displays (Ambady, Conner & Hallahan, 1999) and can be judged more accurately in men (Johnson, Reichman & Tassinary, 2007). Such evidence suggests that gait differences may exist between homosexuals and heterosexuals that might influence perceptions and biomechanical characteristics, thus making this a logical avenue of study.

The development of many male traits pertinent to sexual selection, both inter- and intra-sexually, are thought to be under the influence of T. Prenatal T (PT) in particular has been linked to male performance in many sporting actives such as performance in endurance running (Manning et al., 2007), surfing (Kilduff, et al, 2001), fencing (Voracek et al., 2006), rugby (Bennett et al., 2010), sumo wrestling (Tamiya, et al., 2012) and sprinting (Manning & Hill, 2009). It is hypothesised that PT has had organisational effects on the cardiovascular (Manning & Taylor, 2001; Manning, et al., 2007), nervous and musculoskeletal (Voracek et al., 2006; Kilduff, et al, 2001) systems that is attributed to performance in such sporting endeavours. PT is also thought to provide organisational effects on the male face, thus producing masculinized structures such as an increased jaw size, more robust jaw shape, and prominent brow ridges (Keating et al., 1981; Thornhill & Gangestad, 1996; Grammer et al., 2003), which has led researchers to hypothesise that PT underlies many traits of interest for sexual selection (Neave et al., 2003). Given that T has positive effects on physical performance in sport, and has links to all of the traits investigated in this thesis (health,

cardiovascular fitness, strength and age), an investigation into PT's role in movement quality seems a logical extension of this thesis. Indeed Fink et al., (2007) has previously found links between 2D:4D (a proxy for PT effects) and female ratings of male dance quality; although whether this has effects on biomechanical characteristics of dance is currently unknown.

A consideration based on the findings of this thesis is to further probe the role intra-sexual selection plays in the signalling capacity of human movements. Whilst inter-sexual explanations for female preferences of male traits are widely researched, the ability for males to detect cues in other males in order to assess traits pertinent to intra-sexual competitions is generally under-researched. Because of the conspicuous nature of movement alongside its notable relationship with condition should provide males with cues to formidability and potentially dominance.

A final limitation is that the question of cultural differences was not explored in this thesis because of the relatively homogenous sample of dancers and raters who volunteered to take part. Thus, questions pertaining to whether culture plays a significant role in perceptions of dance quality, especially perceptions of dancing from different cultures remains untested to date. It is known that culture, context and musical style play a large role in the style of dance (Kurath, 1960; Kaeppler, 1978) and is well documented worldwide (Hanna, 2010). However, despite the gap in this thesis pertaining to culture, Hannah (2010) argues that whilst the forms of dance may differ (both intra and inter culturally), they communicate common meanings of sexuality, gender and identity and all forms of dance typically show emphasis of secondary sexual characteristics such as the pelvis and upper body. Also, one might predict that if dance quality provides cues to physical condition, ratings may be similar in mixed culture samples as common components in the dance may be seen as universally of 'good quality' (much the same as research concerning facial attractiveness; Rhodes et al., 1998). Nonetheless, it is clear given the diverse nature of dancing styles worldwide that the

biomechanical makeup of such dances will differ greatly making the biomechanical characteristics making up such quality ratings difficult to investigate.

7.4. Overall Conclusions

In conclusion, movement as a cue to male reproductive quality is chronically under researched to date despite overwhelming attention being paid to static cues. In the animal kingdom dynamic cues have received quite a lot of attention comparatively and vigorous, skilful male displays are quite well documented and are thought to signal condition. This has led to the hypothesis that the artistic form of dance in humans similarly may convey qualities of interest to observers.

This thesis firstly sought to develop a robust methodology for testing the signalling capacity of human movement which eliminates cues known to influence mate choice perceptions such as height, build and attractiveness whilst maintaining a highly realistic human form. This objective has successfully been achieved as evidenced through both validation of such a method against known robust perceptual tasks such as sex recognition and empirical studies investigating honest cues.

The next objective in this thesis was to discover if particular movements or biomechanical characteristics were mediating the relationship between observer's perceptions and traits of interest. This was also achieved as it was discovered that the size and variability of movements of the upper body, arms and overall speed were particularly important predictors in studies reported in this thesis. Furthermore, in one study mediation was observed whereby movements of the central body explained a fair amount of the variance between male perceptions of strength and male observers' ratings of the dance quality.

A final (and particularly important) objective of this thesis was to utilise this novel, cutting edge methodology to investigate cues known to be of interest to females. This too has been successfully achieved and female perceptions of dance quality have been positively related to physical strength. Also, a negative correlation was observed between female perceptions of masculinity and the actual age of a male dancer thus providing evidence that physical condition may be encoded into the dance movements potentially following the pattern of testosterone decline with age. In the final two studies male raters were recruited following an influential paper suggesting males as well as females should have access to traits that have evolved via sexual selection. It was found that male raters showed a positive correlation between their perceptions of dance quality and the physical strength of a male dancer as well as finding that male raters could directly perceive the strength and age in male dance.

In final conclusion, this thesis has developed a cutting edge, novel methodology in which to record movement with clinical accuracy whilst maintaining a highly realistic form. Using this new methodology, exploration into the signalling capacity of male dance movements has been conducted with the ability to investigate whether specific movements are conveying or cueing this information. It was found that aspects of condition such as age and strength could be detected by observers via their perceptions of dance quality, masculinity and age. Furthermore for the first time, quantitative analysis (biomechanical) of movement was conducted which has revealed that larger, more variable movements of the upper body and arms as well as overall speed of movement are important predictors of dance quality ratings and that the chest in particular partially mediates the relationship between ratings of dance quality and physical strength. Other novel findings include a direct relationship between male ratings of age and the actual age of a dancer and a negative relationship between masculinity and the actual age of a dancer by female raters. The

extensive scope and novel findings in this study have resulted in a multitude of rich research avenues to explore thus ensuring research in this field gains much needed momentum.

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Appendices

Appendix A: Methodological Details

Table 1: Plug-In-Gait marker names and their distribution on the Motionbuilder Actor model.

Actor Body Segment	Plug-In-Gait Marker
Head	LFHD (left front head)
	LBHD (left back head)
	RFHD (right front head)
	RBHD (right back head)
Shoulders (Left & Right)	LSHO (left shoulder)
	RSHO (right shoulder)
Upper Body Segment	C7 (upper back)
	T10 (lower back)
	CLAV (clavicle)
	STRN (sternum)
	RBAK (upper right back)
Waist/Hip Segment	LASI (front left hip)
	RASI (right front hip)
	LPSI (back left hip)
	RPSI (back right hip)
Upper Arm (Left & Right)	LUPA (left upper arm)
	RUPA (right upper arm)
	LELB (left elbow)
	RELB (right elbow)
Forearm (Left & Right)	LFRM (left forearm)
	RFRM (right forearm)
	LWRA (left inside wrist)
	LWRB (left outside wrist)
	RWRA (right inside wrist)
	RWRB (right outside wrist)
Hand (Left & Right)	LFIN (left finger)

	RFIN (right finger)
Upper Leg (Left & Right)	LTHI (left thigh)
	RTHI (right thigh)
	LKNE (left knee)
	RKNE (right knee)
Lower Leg (Left & Right)	LTIB (left tibia)
	RTIB (right tibia)
Foot (Left & Right)	LHEE (left heel)
	LANK (left ankle)
	RHEE (right heel)
	RANK (right ankle)

N.B LTOE/RTOE markers were not used

Appendix B: Unpublished health questionnaire

Please indicate how many times you have had each of the following health complaints

		0	1	2	3	4
		Have never experienced	***3 or 4 times per year***	***Every month or so***	***Every week or so***	***More than once a week***
1)	Colds or flu	☐	☐	☐	☐	☐
2)	Athletes foot	☐	☐	☐	☐	☐
3)	Wheezing	☐	☐	☐	☐	☐
4)	Mouth ulcers	☐	☐	☐	☐	☐
5)	Sore throats	☐	☐	☐	☐	☐
6)	Fungal infections	☐	☐	☐	☐	☐
7)	Headaches	☐	☐	☐	☐	☐
8)	Constipation	☐	☐	☐	☐	☐
9)	Diarrhoea	☐	☐	☐	☐	☐
10)	Heart burn	☐	☐	☐	☐	☐
11)	Itchy eyes	☐	☐	☐	☐	☐
12)	Difficulty sleeping	☐	☐	☐	☐	☐
13)	Feeling tired	☐	☐	☐	☐	☐
14)	Feeling thirsty	☐	☐	☐	☐	☐
15)	Feeling hungry	☐	☐	☐	☐	☐
16)	Feeling too hot	☐	☐	☐	☐	☐
17)	Feeling too cold	☐	☐	☐	☐	☐
18)	Itchy / dry skin	☐	☐	☐	☐	☐
19)	Sneezing without a cold	☐	☐	☐	☐	☐
20)	Blocked / runny nose without a cold	☐	☐	☐	☐	☐

MHCQ SCORE _____

Placeholder for Lab Diagram

Glossary

Glossary of Terms

2D:4D. Second to fourth digit ratio. A proxy measure of prenatal testosterone in utero. Lower ratios indicate higher exposure.

FA. Fluctuating Asymmetry. A measure of developmental stability based on the apparent differences in size between bilateral structures of the body. Low symmetry is typicall attributed to robust genes.

fMRI. Functional Magnetic Resonance Imaging. A brain imaging technique that measures the blood concentration to map functioning of specific brain regions by detecting the difference in magnetic fields as a result of high haemoglobin.

MT. Middle Temporal Area. A brain area on the border of the occipital and temporal lobes that preferentially responds to all movement stimuli.

MTG. Medial Temporal Gyrus. A region in the temporal lobe that seems to show preferential activation for tool use.

PL. Point-Light. A method of capturing movement on video whilst minimising structural cues (such as attractiveness). A series of lights are attached to joints and structures of the body during filming and the resulting tape is altered to show only the points.

pSTS. Posterior Superior Temporal Sulcus. See STS

PET. Positron emission topography. Internal body imaging technique in which a radioactive isotope is injected into the blood stream that can be mapped by a special scanner.

rTMS. Repetitive transcranial magnetic stimulation. A non invasive brain investigation technique whereby a magnetic coil is placed over the persons skull that temporarily disrupts or excites the electrical activity of specific brain sites in order to investigate their role in activities.

STS. Superior Temporal Sulcus. A brain structure located in the temporal lobe of the brain. The structure appears to be related to perception of emotion and biological movement.

T. Testosterone. Androgen hormone typically associated with anabolic effects on the muscles and masculinisation of physical features and behaviour. Sometimes differentiated between prenatal (organising) testosterone and circulating) testosterone (attributed to aggressive and dominant behaviour).

V1. Visual area 1, located in the occipital lobe, this brain region is where visual information from the eyes culminates and represents the first stop for visual information processing.

V5. see MT.

Software Glossary

AutoDesk MotionBuilder (2009, 2010, 2012). Professional animation software that allows for the mapping of an avatar (virtual person) to optical motion capture data. The avatar standardises the height and build of the motion data.

Vicon Nexus (v1.05 - v1.7). Motion capture software that integrates with capture hardware to record movement by detecting reflections of round reflective markers placed on the joints of the body. Nexus software is used for the post-processing of capture data to 'clean' the data. It

also allows for the extraction of biomechanical coordinates based on standardised gait models.

Mathworks MATLAB (v2011a). A programming language that allows for extremely large datasets that would not normally be supported by other statistical/data handling programs (e.g. SPSS/Excel) to be processed using a set of programming rules. It was used in this project to reduce large biomechanical files of individual coordinates to more meaningful data.

CamStudio. A freeware program used to record what is being conducted on a computer screen. In this project it was used to create a standardised recording of the avatar moving in AutoDesk MotionBuilder as this program did not natively have a video encoder. Xvid was used as a compressor to reduce file size.

SolveigMM AVI Trimmer. A freeware program used to trim .AVI files to the desired size. In this project all avatars were trimmed to the middle 15 seconds of each dance.

Empirisoft MediaLab (v2008a). An experiment builder program used to present participants with the dance video files and record their perceptions using Likert-style scales into common comma-separated files. Also allowed for the randomisation of videos presented.